An fMRI study of visual hemifield integration and cerebral lateralization

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ABSTRACT

The human brain integrates hemifield-split visual information via interhemispheric transfer. The degree to which neural circuits involved in this process behave differently during word recognition as compared to object recognition is not known. Evidence from neuroimaging (fMRI) suggests that interhemispheric transfer during word viewing converges in the left hemisphere, in two distinct brain areas, an "occipital word form area" (OWFA) and a more anterior occipitotemporal "visual word form area" (VWFA). We used a novel fMRI half-field repetition technique to test whether or not these areas also integrate nonverbal hemifield-split string stimuli of similar visual complexity. We found that the fMRI responses of both the OWFA and VWFA while viewing nonverbal stimuli were strikingly different than those measured during word viewing, especially with respect to half-stimulus changes restricted to a single hemifield. We conclude that normal reading relies on left-lateralized neural mechanisms, which integrate hemifield-split visual information for words but not for nonverbal stimuli.

1. Introduction

Due to the division of neural fibers from the nasal hemiretinae in the optic chiasm and uncrossed fibers from the temporal hemiretinae, sensory information available in each visual hemifield is initially projected to the contralateral occipital lobe and subsequently combined via interhemispheric transfer. In addition to its role in binocular vision (Mitchell and Blakemore, 1970), interhemispheric transfer plays an integral role in word recognition (Brysbaert, 2004; Hunter et al., 2007; Monaghan and Shillcock, 2008), face perception (Bridgman et al., 2014; Hsiao et al., 2008), the detection of mirror symmetry (Herbert and Humphrey, 1996; Saarinen and Levi, 2000) and other forms of perceptual organization (Genç et al., 2011; Pillow and Rubin, 2002). The precise nature of mechanisms involved in the hemispheric integration of foveal input is controversial (Ellis and Brysbaert, 2010), but hemispheric transfer is necessary for the neural integration of all hemifield-split visual input, even within a degree of visual angle from the vertical midline of the visual field (Berlucchi, 2014; Reinhard and Trauzettel-Klosinski, 2003). Given the reliance of reading upon visual processing within this range of the visual field, interhemispheric transfer clearly plays an integral role in the neural integration of hemifield-split words during reading (Dougherty et al., 2005; Lavidor and Walsh, 2004), and its disruption is associated with dyslexia (Henderson et al., 2007).

Recently, Strother et al. (2016) used functional MRI (fMRI) to reveal a hemispheric asymmetry in the visual integration of letters comprising a word split at fixation. Specifically, they reported an "occipital word form area" (OWFA), which contains neurons that bind hemifield-split word parts into a unitary bilateral hemifield word form representation. Their finding suggests that this process occurs earlier in visual cortex than proposed by models of hemifield integration in an anatomically anterior occipitotemporal "visual word form area" (VWFA; Cohen et al., 2003; Molko et al., 2002). Based on the Talairach coordinates reported by Strother et al., the OFA/OWFA is located either within or near the inferior occipital gyrus, intermediate to V4v (hV4) in the transverse collateral sulcus (Witthoft et al., 2014), and object-selective neurons on or near the lateral occipital gyrus (Larsson and Heeger, 2006; Strother et al., 2010), possibly corresponding to a coarsely retinotopic putative human posterior inferior temporal area (phPIT) or a putative V4 transitional (pV4t) zone (Kolster et al., 2010). In contrast, the VWFA is considerably more anterior, in fusiform cortex (lateral to the middle section of the fusiform gyrus), typically lateral and/or anterior to visual field maps VO-1 and VO-2, and inferior and medial to visual field maps TO-1 and TO-2 (Yeatman et al., 2013). Strother et al. showed that the OWFA in left occipital cortex was precisely symmetric in anatomical location relative to an "occipital face area" (OFA; Gauthier et al., 2000) in the right hemisphere. The OFA is typically larger and more frequently found in the right hemisphere (Pitcher et al., 2011), and it represents visual features of faces and spatial relations between them during the early stages of processing (Liu et al., 2010; Pitcher et al., 2007; Rhodes et al., 2009; Strother et al., 2011). The right OFA is distinct from its more elusive left counterpart in its sensitivity to mirror

and its role in interhemispheric integration during face recognition (Bona et al., 2015; Frässle et al., 2016; Kietzmann et al., 2015).

In addition to a growing interest in the parallels between word recognition and the visual processing of faces (Behrmann and Plaut, 2013; Dehaene et al., 2015, 2010; Nestor et al., 2013), there is also considerable longstanding interest in the degree to which potentially word-specific mechanisms are engaged during the visual processing of nonverbal stimuli (Seghier and Price, 2011; Vogel et al., 2012, 2014). Given the antipodal anatomical relationship between the right OFA and the OWFA reported by Strother et al. (2016), it is reasonable to expect that the role of the OWFA in word recognition exhibits some parallels with the role of the OFA in face perception, such as the representation of constituent "parts" of a configuration. A limitation of the study by Strother et al. is that the authors did not test whether or not the OWFA integrates hemifields-split parts of non-word configurations. Here we report results from two experiments that employed the same fMRI method used by Strother et al., and an original reanalysis of a subset of their data, to show that both the OWFA and the VWFA selectively bind hemifield-split letters of a word but not non-letter parts of nonverbal configurations. Specifically, we used non-verbal stimuli, which either repeated or changed in full, or repeated/changed on one half or the other. Our logic in using these conditions was the same as Strother et al. Suppression of fMRI responses should only occur for neural populations in the hemisphere contralateral to the hemifield location of repetition unless these neurons receive ipsilateral input (e.g. via the corpus callosum); we were specifically interested in asymmetries of contral-ateral and ipsilateral hemifield-specific repetition suppression or re-lease from suppression. Our results are consistent with results of some previous studies of the VWFA, but emphasize the role of more posterior regions of visual cortex, the OWFA in particular. Our results also emphasize the utility of half-field manipulations of hemifield-split stimuli in conjunction with fMRI, which can improve our understanding of word recognition and also the process of inter-hemifield integration in object recognition more generally.

2. Material and methods

2.1. Participants

Twelve right-handed volunteers (21–27 years of age; 8 female) participated in Experiment 1; the subjects were a subset of those who participated in the study by Strother et al. (2016). Twelve different right-handed observers (20–33 years of age; 9 female) participated in Experiment 2. All participants were literate native English speakers and were literate in English only. All participants were recruited from the University of Western Ontario (London, Ontario, Canada), and all consent forms and experimental procedures described in these forms were approved by the University of Western Ontario's research ethics board.

2.2. fMRI data acquisition and analysis

Imaging was conducted at the Robarts Research Institute (London, Ontario, Canada) using a 3-T Siemens Tim MAGNETOM Trio imaging system. BOLD data were collected using T2*-weighted interleaved, single segment, EPI, PAT = 2, and a 32-channel head coil (Siemens, Erlangen, Germany). Foam padding was used to reduce head motion. Functional data were aligned to high-resolution anatomical images obtained using a 3-D T1 MPRAGE sequence (echo time [TE] = 2.98 ms; repetition time [TR] = 2300 ms; inversion time = 900 ms; flip angle = 9°; 192 contiguous 1 mm slices; field of view = 240 × 256 mm^2). Each functional volume included 33 contiguous slices. Scanning parameters for obtaining functional data with full coverage of OT: TE = 30; TR = 2 s (single shot); flip angle = 90°; field of view = 148 × 148 mm^2; 2 × 2 × 2 mm^3 voxel size. Each run of the main experiment included 204 volumes.

Data were preprocessed and analyzed using BrainVoyager QX 2.1 (BVQX; Brain Innovation, Maastricht, The Netherlands). We performed corrections for slice scan time, head motion (always < 2 mm), and low-frequency artefactual drift (linear trend removal and high pass filter of 3 cycles/run); each functional volume for a given participant was aligned to the functional volume collected closest in time to the anatomical volume. Functional data were superimposed on anatomical brain images, aligned on the AC–PC line, and transformed into Talairach (Talairach et al., 1988) space and co-registered with the anatomical image for each participant. Talairach transformation was performed using standard BVQX procedures (Goebel, 1996). The hemispheres were segmented at the gray/white matter boundary, and the resultant cortical sheet was then reconstructed, inflated, and flattened for functional data analyses and visualization. Functional data were spatially smoothed using a Gaussian kernel of 8 mm (FWHM). Predictors were generated using rectangular wave functions (with a value of 1 for l volume = 2 s when the action was initiated at the onset of the inter-trial interval and a value of 0 for the remainder of the trial) that were convolved with a hemodynamic response function (Boynton et al., 1996).

2.3. Stimuli and procedure

Both Experiment 1 and 2 employed the same general procedure as Strother et al. (2016), but with different stimuli. Fig. 1 shows stimuli and conditions from the Strother et al. experiment and the experiments reported here. All *word* (Fig. 1a), *silhouette* (Fig. 1b), and *Japanese character* (Fig. 1c) stimuli extended to a visual angle of ~5° × 1.5° (viewed via mirror at 15 cm distance). In all cases, observers fixated a small (~0.05°) dot centered on the screen. Silhouette string stimuli in Experiment 1 were comprised of four animal shapes. The Japanese character stimuli used in Experiment 2 were comprised of four different characters (including Kanji and Kana), and were roughly equated in spatial frequency to the word stimuli in the previous study (but not the silhouettes in Experiment 1). All stimuli were split in half between the left (LVF) and right (RVF) visual hemifields.

As in Strother et al., four experimental conditions were used in each experiment: *Same*, *Different*, *RVF change*, and *LVF change*. A 12-s block design was adopted for both experiments identical to the previous study, and within each block, 12 stimuli were presented at a rate of 1 Hz, with words/strings displayed cyclically (until the end of a 12 s block) for 500 ms followed by 500 ms blank screen. For the *Same* condition, each block contained the same four string components repeated for 12 times. For the *Different* condition, each block contained 12 different stimuli changing in both LVF and RVF. For the *RVF change* condition, each block contained 12 stimuli with the same stimulus repeated in the LVF, but changing stimuli in the RVF, and vice versa for the *LVF change* condition. There were 34 blocks in each run, and 8 blocks per condition with 2 fixation blocks (1 block in the beginning and 1 block at the end). Ninety-six words sharing the left two letters and ninety-six words sharing the right two letters were used as stimuli in the Strother et al. experiment (stimuli for *Same* and *Different* conditions were subsets of these); twelve different words sharing the
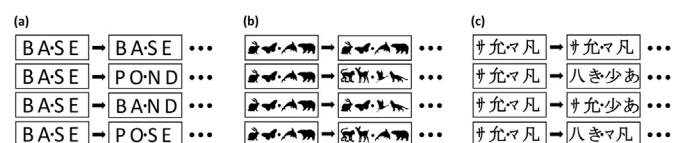

Fig. 1. Stimuli and conditions used in Strother et al. (2016) and Experiments 1 and 2: (a) words; (b) silhouettes; and (c) Japanese character strings. The top row shows paired examples of Same (repeated) stimuli. The second row shows examples of Different (non-repeating) stimuli. The third and bottom rows show RVF and LVF change stimuli, respectively, for which half the string repeats and half changes between successive presentations within a block. Note that although pairs are shown here, blocks contained sequences of twelve stimuli (indicated by dots).
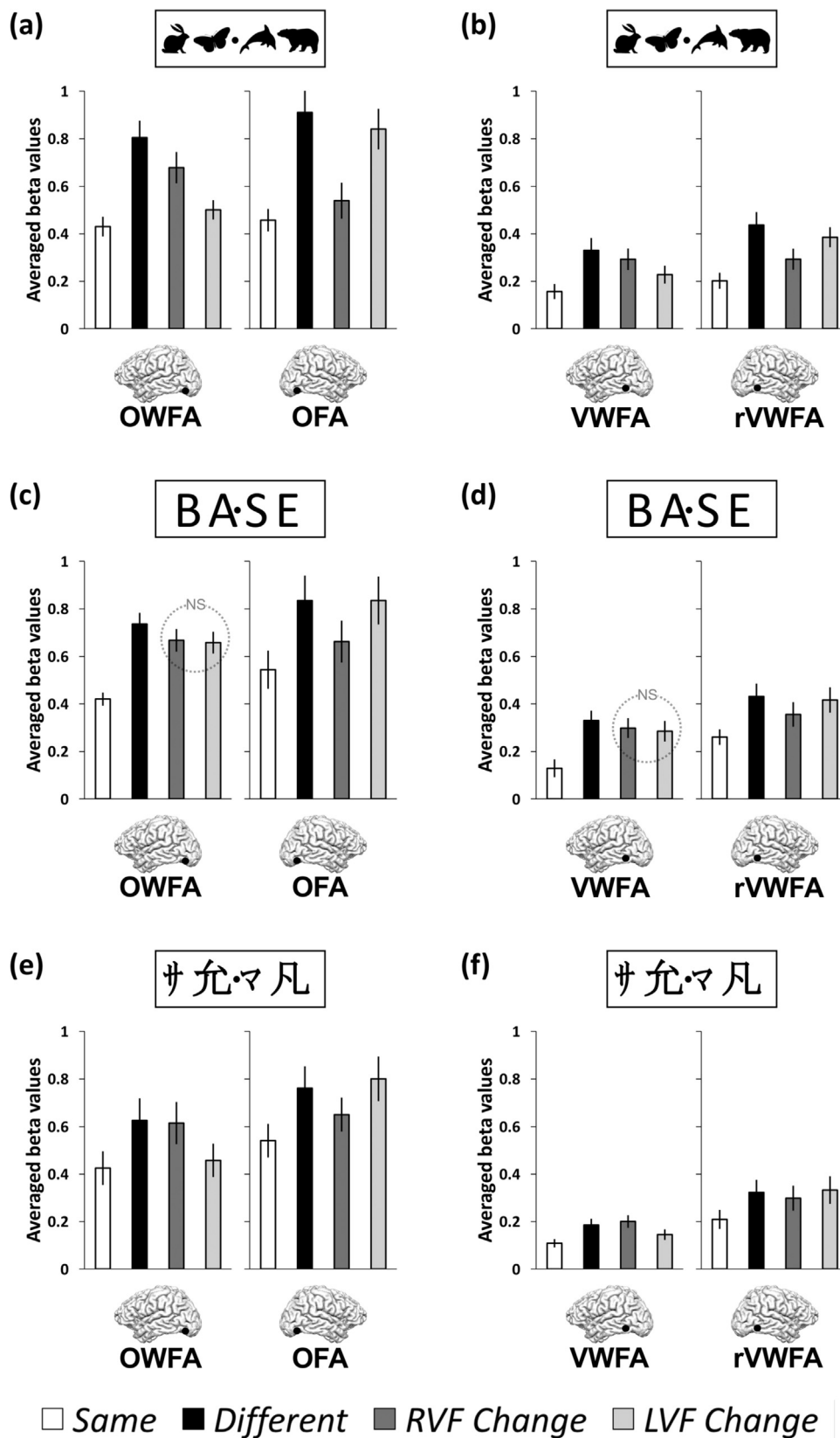
Fig. 2. Results of ROI analyses from Experiment 1 (top row), Strother et al. (2016; second row), and Experiment 2 (bottom row). Four ROIs are paired by OWFA and OFA (left), and by VWFA and rVWFA (right). All ROIs show repetition suppression (Different > Same) for Experiment 1, Strother et al. (2016), and Experiment 2. Importantly, in Experiment 1, (a) and (b), and 2, (e) and (f), all ROIs show contralateral bias for half change nonverbal stimulus (RVF change > LVF change in the OWFA and VWFA, LVF change > RVF change in the OFA and rVWFA). However, in Strother et al. (2016), (c) and (d), the OWFA and VWFA show equal fMRI responses to both left and right half-word changes (dashed circle; RVF change = LVF change) while the OFA and rVWFA still exhibit contralateral bias to left half-word change (LVF change > RVF change). "NS" refers to a lack of significant difference when using a liberal statistical test (see text for details).

same first or last two letters were used in each block (12×8 blocks per run = 96 total). Silhouette and Japanese character stimuli were created by substituting single silhouettes or characters with each letter in the word stimuli. In all experiments, block order was counterbalanced across runs and each volunteer participated in a minimum of four runs.

3. Results

3.1. ROI analyses

We were primarily interested in the OWFA and VWFA reported by Strother et al. (2016). We therefore present region of interest (ROI) analyses of the OWFA and VWFA, and their anatomical counterparts in the right hemisphere, for each of the two new experiments and reanalyzed results from the Strother et al. study. Some of our results are reported in Supplementary Materials. We also report results from group-level whole brain analyses, both here and in Supplementary Materials.

We defined the OWFA and its right hemisphere counterpart based on anatomically mirror symmetric Talairach coordinates of the OFA reported by Strother et al. (2016). The OFA coordinates reported in their study were obtained in an independent experiment from their main study, the results of which we compare to those obtained in the new experiments reported here (i.e., our ROI definitions are not based on any of the fMRI results reported here, thus avoiding circularity and lack of independence). The OWFA ROI was centered at Talairach coordinates $x = -39$, $y = -80$, $z = -10$, anatomically mirror symmetric to the OFA ($x = 39$, $y = -80$, $z = -10$) reported by Strother et al. Rather than use the VWFA coordinates reported by Strother et al. (which was not defined using an independent localizer in their study), we defined the coordinates of our VWFA ROI based on coordinates reported by Glezer et al. (2015), transformed from MNI ($x = -42$, $y = -58$, $z = -17$) to Talairach coordinates ($x = -40$, $y = -59$, $z = -10$); we also defined an anatomically mirror symmetric right hemisphere VWFA (rVWFA) centered at 40, $y = -59$, $z = -10$. All ROIs consisted of a ~800-voxel cube centered on the reported Talairach coordinates from which fMRI beta values were extracted for analysis.

3.1.1. ROI analyses for Experiment 1 (silhouettes)

Fig. 2a shows average beta values for all conditions, for the OWFA and OFA from Experiment 1 (silhouettes). A two-way repeated measures ANOVA was conducted on betas for each condition (*Same*, *Different*, *RVF change*, and *LVF change*) and ROI (OWFA and OFA), followed by paired tests with Bonferroni correction for multiple comparisons. The ANOVA results showed a main effect of condition, $F(3, 33) = 46.39$, $p < 0.001$, and an interaction between condition and ROI, $F(3, 33) = 33.08$, $p < 0.001$. The main effect of ROI was not significant, $F(1, 33) = 1.13$, $p = 0.31$.

Results from all paired comparisons are reported in Supplemental Materials (Table S.1). We were mainly interested in comparisons of betas between the *Same* and *Different* conditions, and the *RVF change* and *LVF change* conditions. In the OWFA, *Different* betas ($M = 0.804$, $SE = 0.072$) were significantly larger than *Same* betas ($M = 0.430$, $SE = 0.041$), $p < 0.001$; and in the OFA, *Different* betas ($M = 0.910$, $SE = 0.092$) were also significantly larger than *Same* betas ($M = 0.457$, $SE = 0.047$), $p < 0.001$. These results suggest significant repetition suppression in both the OWFA and OFA for silhouettes.

We were especially interested in whether or not the OWFA and OFA would show different magnitudes of fMRI response to the *RVF change* and *LVF change* conditions. Bonferroni-corrected paired comparisons confirmed significant differences in both ROIs: in the OWFA, *RVF change* betas ($M = 0.668$, $SE = 0.066$) were significantly larger than *LVF change* betas ($M = 0.500$, $SE = 0.040$), $p < 0.01$; and in the OFA, *LVF change* betas ($M = 0.840$, $SE = 0.086$) were significantly larger than *RVF change* betas ($M = 0.539$, $SE = 0.076$), $p < 0.001$. In short, the results showed that the OWFA and OFA responses to the two change conditions

were not the same, but rather, showed a contralateral bias (contralateral > ipsilateral fMRI responses). Results of all possible paired comparisons are summarized in Table S.1.

Fig. 2b shows results for the VWFA and rVWFA from Experiment 1 (silhouettes). A two-way repeated measures ANOVA was conducted prior to paired comparisons. The results showed a main effect of condition, $F(3, 33) = 22.01$, $p < 0.001$, and an interaction between condition and ROI, $F(3, 33) = 16.63$, $p < 0.001$. The main effect of ROI was marginally significant, $F(1, 33) = 4.32$, $p = 0.062$. Paired comparisons with Bonferroni correction (see Table S.1) indicated that, in the VWFA, *Different* betas ($M = 0.330$, $SE = 0.052$) were significantly larger than *Same* betas ($M = 0.156$, $SE = 0.032$), $p < 0.005$; and in the rVWFA, *Different* betas ($M = 0.436$, $SE = 0.054$) were also significantly larger than *Same* betas ($M = 0.202$, $SE = 0.034$), $p < 0.001$. This means repetition suppression occurred in both the VWFA and the rVWFA for nonverbal string stimuli.

As in the OWFA and OFA, we were mainly interested in whether or not the VWFA and rVWFA would show different fMRI responses to the *RVF change* and *LVF change* conditions. In the VWFA, paired comparison revealed that *RVF change* betas ($M = 0.292$, $SE = 0.045$) were not significantly differ from *LVF change* betas ($M = 0.227$, $SE = 0.037$), $p = 0.11$; in the rVWFA, *LVF change* betas ($M = 0.385$, $SE = 0.042$) were significantly larger than *RVF change* betas ($M = 0.292$, $SE = 0.044$), $p < 0.001$. In addition to our Bonferroni-corrected paired comparisons we conducted an additional considerably more liberal statistical test for non-significant paired comparison – a one-sample t-test (one-tailed) based on a contralateral sensitivity index (CSI), computed by subtracting the fMRI responses to *LVF change* from *RVF change* (for the left hemisphere ROIs, OWFA and VWFA) or subtracting the fMRI responses to *RVF* change from *LVF change* (for the right hemisphere ROIs, OFA and rVWFA), and dividing by their sum (i.e. $\text{CSI}_{\text{Left}} = (R_{RVF\ change} - R_{LVF\ change})/(R_{RVF\ change} + R_{LVF\ change})$; $\text{CSI}_{\text{Right}} = (R_{LVF\ change} - R_{RVF\ change})/(R_{LVF\ change} + R_{RVF\ change})$). The result showed significant differences for the VWFA, $t(11) = 2.09$, $p = 0.03$. In short, the VWFA and rVWFA both showed greater fMRI responses to contralateral half-stimulus changes as compared to ipsilateral half-stimulus changes, although not to the same degree (statistical significance for the rVWFA test survived Bonferroni correction whereas that for the VWFA did not); this will be important in subsequent between-experiment comparisons of ROI results. To summarize the results of our analyses, we observed repetition suppression in all ROIs, and also a contralateral bias in all ROIs.

3.1.2. Reanalyzed results from Strother et al. (2016)

The 12 participants in Experiment 1 comprised a subset of the 18 participants who participated in the split-words study by Strother et al. (2016). Our main goal was to characterize the similarities and differences between the two experiments in the same set of participants, with a particular focus on beta values in the *RVF change* and *LVF change* conditions, which Strother et al. did not compare directly their published study. We also present results for overall repetition suppression.

Fig. 2c shows results for the OWFA and the OFA of a reanalysis of data from Strother et al. (same 12 subjects as Experiment 1). We again performed a two-way repeated measures ANOVA, which showed similar results to those observed in Experiment 1 (a main effect of condition, $F(3, 33) = 40.42$, $p < 0.001$, and an interaction between condition and ROI, $F(3, 33) = 8.68$, $p < 0.001$). The main effect of ROI was not significant, $F(1, 33) = 1.05$, $p = 0.33$. Subsequent paired comparisons results are shown in Table S.2. In the OWFA, *Different* betas ($M = 0.736$, $SE = 0.048$) were significantly larger than *Same* betas ($M = 0.420$, $SE = 0.028$), $p < 0.001$; and in the OFA, *Different* betas ($M = 0.834$, $SE = 0.105$) were significantly larger than *Same* betas ($M = 0.543$, $SE = 0.080$), $p < 0.001$. Additional paired comparisons showed that *RVF change* betas ($M = 0.667$, $SE = 0.047$) were not significantly different from *LVF change* betas ($M = 0.657$, $SE = 0.046$), $p = 1.00$. Unlike the OWFA, *LVF change* betas ($M = 0.835$, $SE = 0.101$)

were significantly larger than *RVF change* betas ($M = 0.661$, $SE = 0.088$) in the OFA, $p < 0.005$. We performed a more liberal statistical test on the non-significant results using the CSI. Unlike our corresponding result for Experiment 1, the result of this one-sample *t*-test on the CSI was still not significant: $t(11) = 0.40$, $p = 0.35$ (one-tailed). In Fig. 2c, the "NS" refers to non-significance in this more liberal statistical test, and we interpret it to suggest a lack of contralateral bias in the OWFA for half-word changes.

Fig. 2d shows results for VWFA and rVWFA. We performed a two-way repeated measures ANOVA on betas for condition and ROI, which showed a main effect of condition, $F(3, 33) = 40.06$, $p < 0.001$, and an interaction between condition and ROI regions, $F(3, 33) = 3.80$, $p = 0.019$. The main effect of ROI region was marginally significant, $F(1, 33) = 4.62$, $p = 0.055$. All of the following paired comparisons are reported in Table S.2. In the VWFA, *Different* betas ($M = 0.736$, $SE = 0.048$) were significantly larger than *Same* betas ($M = 0.420$, $SE = 0.028$), $p < 0.001$; and in the rVWFA, *Different* betas ($M = 0.431$, $SE = 0.054$) were significantly larger than *Same* betas ($M = 0.260$, $SE = 0.033$), $p < 0.001$.

In the VWFA, paired comparison revealed that *RVF change* betas ($M = 0.298$, $SE = 0.042$) did not differ from *LVF change* betas ($M = 0.284$, $SE = 0.044$), $p = 1.00$; and in the rVWFA, *LVF change* betas ($M = 0.416$, $SE = 0.054$) were larger than *RVF change* betas ($M = 0.355$, $SE = 0.052$), $p = 0.015$. When we used a more liberal one-sample *t*-test using the CSI (one-tailed), the result showed that the CIS for the VWFA was still not significant, $t(11) = 0.89$, $p = 0.39$ (Fig. 2d, "NS"). Taken together, the VWFA (like the OWFA) showed equivalent fMRI responses to *RVF change* and *LVF change* for words, but not for silhouettes (Experiment 1), whereas the rVWFA showed a clear contralateral bias for LVF versus RVF half-word changes.

3.1.3. ROI analyses for Experiment 2 (Japanese characters)

Fig. 2e shows results for the OWFA and OFA from Experiment 2 (Japanese characters). We again performed a two-way repeated measures ANOVA, which showed a main effect of condition, $F(3, 33) = 24.72$, $p < 0.001$, a main effect of ROI, $F(1, 33) = 7.75$, $p < 0.05$, and an interaction between condition and ROI, $F(3, 33) = 32.52$, $p < 0.001$. The main effect of ROI indicates that fMRI responses in the OWFA were lower than those in the OFA. All of the following paired comparisons are reported in Table S.3. Paired comparisons with Bonferroni correction indicated that, in the OWFA, *Different* betas ($M = 0.625$, $SE = 0.093$) were larger than *Same* betas ($M = 0.425$, $SE = 0.071$), $p < 0.001$; and in the OFA, *Different* betas ($M = 0.761$, $SE = 0.092$) were significantly larger than *Same* betas ($M = 0.540$, $SE = 0.071$), $p < 0.001$. Additional paired comparisons showed that *RVF change* betas in the OWFA ($M = 0.614$, $SE = 0.089$) were larger than *LVF change* betas ($M = 0.457$, $SE = 0.070$), $p = 0.014$; and in the OFA, *LVF change* betas ($M = 0.800$, $SE = 0.094$) were significantly larger than *RVF change* betas ($M = 0.650$, $SE = 0.071$), $p < 0.005$. Thus, as in Experiment 1 (but not in the reanalyzed data from Strother et al. (2016)), clear contralateral half-change biases were observed in the OWFA and the OFA.

Fig. 2f shows results for the VWFA and rVWFA from Experiment 2 (Japanese characters). A two-way repeated measures ANOVA on betas for condition and ROI revealed: a main effect of condition, $F(3, 33) = 16.38$, $p < 0.001$, a main effect of ROI, $F(1, 33) = 11.87$, $p < 0.005$, and an interaction between condition and ROI, $F(3, 33) = 15.55$, $p < 0.001$. As before, we performed Bonferroni-corrected paired comparisons which are reported in Table S.3. In the VWFA, *Different* betas ($M = 0.185$, $SE = 0.026$) were larger than *Same* betas ($M = 0.108$, $SE = 0.017$), $p = 0.011$; and in the rVWFA, *Different* betas ($M = 0.322$, $SE = 0.053$) were significantly larger than *Same* betas ($M = 0.209$, $SE = 0.040$), $p < 0.005$. Again, we observed repetition suppression in both the VWFA and rVWFA for Japanese characters (as in the OWFA and OFA).

Finally, with respect to contralateral bias for half-stimulus changes, *RVF change* betas in the VWFA ($M = 0.200$, $SE = 0.026$) were larger than

LVF change betas ($M = 0.145$, $SE = 0.022$), $p = 0.014$. In the rVWFA, *LVF change* betas ($M = 0.332$, $SE = 0.058$) did not differ from *RVF change* betas ($M = 0.298$, $SE = 0.053$), $p = 0.16$. We again used one-sample *t*-tests (one-tailed) to examine the CSI for the rVWFA. The result showed a significant effect, $t(11) = 3.04$, $p < 0.01$. In short, the results of these analyses showed a contralateral bias, as observed in Experiment 1, but which was absent in the reanalyzed data of Strother et al. (2016). Comprehensive paired comparisons for this experiment are reported in Supplemental Materials (Table S.4).

3.1.4. Direct comparison of ROIs results between experiments

To this point we have restricted our analyses to each experiment separately from the others. Here directly compare results between all three. Our first analysis investigated the differences in the effects of the contralateral bias to different stimulus types used across experiments for each ROI. A two-way mixed ANOVA on betas for ROI (OWFA and OFA) and experiment (silhouettes, word, and Japanese characters) revealed a main effect of ROI, $F(1, 33) = 4.98$, $p = 0.033$, a main effect of experiment, $F(2, 33) = 11.19$, $p < 0.001$, and a two-way interaction between ROI and experiment, $F(2, 33) = 5.82$, $p < 0.01$. This means the OWFA and the OFA showed different patterns of contralateral sensitivity depending on stimulus type (i.e. experiment), which we clarify next.

As suggested by the individual ROI × experiment analyses performed earlier, in the OWFA, a one-way between subjects ANOVA on the CIS for experiment suggested that there was a significant difference for silhouettes, word, and Japanese characters, $F(2, 33) = 8.76$, $p < 0.001$. Pairwise comparisons with Bonferroni correction indicated that the CSI for word ($M = 0.008$, $SE = 0.020$) was smaller than for silhouettes ($M = 0.137$, $SE = 0.030$) and Japanese characters ($M = 0.155$, $SE = 0.033$), both p values < 0.01, but there was no difference between results for silhouettes and Japanese characters ($p = 1.00$). In the OFA, a one-way between subjects ANOVA suggested that there was also a significant difference for silhouettes, word, and Japanese characters, $F(2, 33) = 7.32$, $p < 0.005$. Pairwise comparisons with Bonferroni correction indicated that CSI for silhouettes ($M = 0.236$, $SE = 0.031$) was larger than for word ($M = 0.132$, $SE = 0.028$) and Japanese characters ($M = 0.093$, $SE = 0.022$), both p values < 0.05, and there was no different between word and Japanese characters, $p = 0.99$. Taken together, these tests further confirm our earlier within-experiment results, which showed that whereas the OWFA showed equivalent sensitivity (CSI = 0.008) to both *RVF change* and *LVF change* for words, but a contralateral bias (CSI > 0.1) for silhouettes and Japanese character, the OFA showed a contralateral bias across all three experiments.

Next, we conducted a two-way mixed ANOVA on the CSI for ROI (VWFA and rVWFA) and experiment (silhouettes, word, and Japanese characters). Unlike the results for the OWFA and OFA across experiments, direct comparison of the VWFA and rVWFA across experiments failed to show any statistically significant differences—no significant effect of ROI ($F(1, 33) = 0.21$, $p = 0.65$), experiment, ($F(2, 33) = 2.33$, $p = 0.11$), or the interaction between ROI and experiment ($F(2, 33) = 0.92$, $p = 0.41$). This means that despite the lack of contralateral bias for half-word changes reported earlier for the VWFA, the VWFA and rVWFA behaved more similarly across experiments – with respect to contralateral bias (i.e., contralateral bias was always relatively weak as compared to the OWFA and OFA) – than did the OWFA as compared to the OFA. This suggests a distinction between the OWFA and VWFA in terms of contralateral sensitivity.

A second analysis investigated the lateralization of the repetition suppression between the OWFA and OFA, or the VWFA and rVWFA across all three experiments. We computed a suppression index (SI) for each ROI, which was defined by subtracting the fMRI responses to *Same* condition from *Different* condition, and dividing by their sum, $SI = (R_{Different} - R_{Same}) / (R_{Different} + R_{Same})$. A two-way mixed ANOVA on SI for ROI (OWFA and OFA) and experiment (silhouettes, word, and Japanese

characters) revealed a main effect of experiment, $F(2, 33) = 4.28$, $p = 0.022$. There was no main effect of ROI, $F(1, 33) = 0.41$, $p = 0.53$, or interaction between ROI and experiment, $F(2, 33) = 1.94$, $p = 0.16$. This indicates that the suppression effect greatest for Experiment 1, but the degree of repetition suppression in Experiment 2 and the reanalyzed data from Strother et al. (2016) were not different from each other. This observation required that we compare using the SI because of overall differences in the magnitude of the BOLD signal between the two experiments.

We repeated the previous analysis (two-way mixed ANOVA) on the SI for ROI (VWFA and rVWFA) and experiment (silhouettes, word, and Japanese characters). We observed a main effect of ROI, $F(1, 33) = 4.51$, $p = 0.041$, and an interaction between ROI and experiment, $F(2, 33) = 4.00$, $p = 0.028$. The main effect of experiment was not significant, $F(2, 33) = 1.07$, $p = 0.36$. Paired comparisons with Bonferroni correction indicated that, in Experiment 1, the SI for the VWFA ($M = 0.316$, $SE = 0.084$) was not significantly different from the SI for the rVWFA ($M = 0.329$, $SE = 0.100$), $p = 0.84$; in the reanalyzed data from Strother et al. (2016), the SI for the VWFA ($M = 0.532$, $SE = 0.093$) was significantly larger than the SI for the rVWFA ($M = 0.256$, $SE = 0.029$), $p = 0.014$; but in Experiment 2, the SI for the VWFA ($M = 0.261$, $SE = 0.104$) was not significantly different from the SI for the rVWFA ($M = 0.236$, $SE = 0.045$), $p = 0.74$.

Taken together, the SI analyses showed evidence of left lateralization of repetition suppression for words, and although right lateralization was not significant in Experiments 1 and 2, we found no evidence of left lateralization in these experiments. We revisit the possibility of right-lateralized repetition suppression for nonverbal stimuli in whole brain analyses in the next section. With respect to contralateral bias, which was of primary interest, our results confirm the lack of contralateral bias in the OWFA. While this was also observed in the VWFA, contralateral bias in the rVWFA was relatively weak as compared to the OFA, consistent with expected decreasing contralateral bias in general moving posterior-to-anterior in visual cortex (Hemond et al., 2007). Furthermore, in contrast to the VWFA, the OWFA showed greater fMRI responses during the *Different* condition as compared to the *RVF change* and *LVF change* conditions (Tables S.1 to S.4 in Supplemental Materials), as reported by Strother et al., although this effect was not limited to words and therefore suggests that OWFA representations may be pre-lexical.

3.2. Whole brain analysis

The goals of the whole brain analysis were to (1) determine the regions showed repetition suppression, (2) search for evidence of lateralization, and (3) investigate the contralateral sensitivity of each hemisphere to the half change stimulus in Experiment 1 and 2, and also in Strother et al. (2016). We reported the whole brain analysis based on three contrasts: *Same > Different*, *RVF change > LVF change*, and *LVF change > RVF change*. A percent signal change transformation and a correction for serial correlations were applied to each participant data, and a random effects GLM was applied to group data. Talairach coordinates of the voxels survived after correction for cluster size (> 10) were reported.

3.2.1. Repetition suppression

We first identified the voxels that showed significant repetition suppression by the different > same contrast based on a false discovery rate q(FDR) of 0.05 for Experiment 1 (which showed the greatest repetition suppression) and the previous study by Strother et al. (Figs. 3a and b, smaller brains in upper left). For Experiment 2, no repetition suppression was found at q(FDR) < 0.05 (i.e., repetition suppression was relatively weaker overall as compared to the other experiments), thus we applied a statistical threshold of $p < 0.005$ uncorrected which yielded roughly equal numbers of voxels as compared to the previous study by Strother et al. (Fig. 3c, smaller brain in

upper left). We then performed voxel counts for each experiment to test for overall lateralization of repetition suppression (recall that in the previous section we focused only on our ROIs).

In Experiment 1, we found that there were 33,905 voxels activated in the left hemisphere with roughly equal numbers of voxels in the right (32,686 voxels) suggesting no lateralization between left and right hemispheres. This is consistent with results from the ROI analysis which also did not find evidence of lateralization in all the ROIs. However, when we applied a more restricted statistical threshold (q(FDR) < 0.005), we observed more voxels were activated in the right hemisphere (numbers of voxels = 4138) than in the left hemisphere (numbers of voxels = 3555), see Figs. S.1a and S.2a in Supplementary Materials. Taken together, the voxel counts show no evidence of left lateralization (consistent with the SI results), but rather, the possibility of right-lateralized repetition suppression for nonverbal silhouettes stimuli.

The whole brain reanalyzed results of our previous study showed that there were fewer voxels activated in Experiment 1 (Fig. 3b), which suggests greater repetition suppression in Experiment 1 (recall that the same 12 participants were included in the both experiments, and the same statistical thresholds were applied (q(FDR) < 0.05)). More importantly, we observed more voxels in the left hemisphere (numbers of voxels = 19025) than in the right hemisphere (numbers of voxels = 16792), which indicates left-lateralized repetition suppression for words (Fig. 3b, small brain in upper left). As before, a more restrict threshold at q(FDR) < 0.005 was applied to the *Different > Same* contrast (Figs. S.1b and S.2b in Supplementary Materials), and we again observed more activation in the left hemisphere (numbers of voxels = 2164) than in the right hemisphere (numbers of voxels = 748). In short, whole-brain analysis showed clear left lateralization of repetition suppression for words, which was not observed in Experiment 1.

In Experiment 3, at the threshold of $p < 0.005$ uncorrected, we found that there were more voxels activated in the right hemisphere (numbers of voxels = 20064) than in the left hemisphere (numbers of voxels = 15018). This right lateralization (2690 voxels in the right hemisphere and 2073 voxels in the left hemisphere) was also evident when we increased the threshold to $p < 0.0005$ uncorrected (Figs. S.1c and S.2c in Supplementary Materials). In short, the whole-brain analysis of the repetition suppression in Experiment 3 showed an overall right lateralization for Japanese character strings, more pronounced than that observed in Experiment 1 (silhouettes); both experiments showed an opposite pattern of lateralization for repetition suppression than the left lateralization observed for words.

3.2.2. Contralateral bias

Our final whole-brain analyses focused on contralateral bias and the prospective relative lateralization of the bias or its absence (i.e., given that the OWFA and VWFA did not show contralateral bias for words). We identified brain regions that showed contralateral bias by the *RVF change > LVF change* and *LVF change > RVF change* contrasts at a statistical threshold of q(FDR) < 0.05. The results showed that left ventral occipitotemporal cortex (vOTC) and right early visual cortex (in the vicinity of visual cortical area V4) were activated for *RVF change > LVF change* and *LVF change > RVF change* contrasts in Experiment 1, respectively. However, this later proved problematic for comparison with Experiment 2 (and the reanalyzed data) because of the relatively small magnitude of the difference between fMRI responses in the *RVF change* versus *LVF change* conditions in these data compared to those from Experiment 1 (as observed in the ROI analyses of CSI reported earlier). When we used a more liberal threshold ($p < 0.01$, uncorrected), equated across experiments (Figs. 3a–c), we observed different patterns of contralateral bias depending on experiment. In Experiment 1 (Fig. 3a), contralateral bias was observed in both hemispheres. In both hemispheres, this overlapped highly with the repetition suppression results (white outlines in Fig. 3a), overlapped
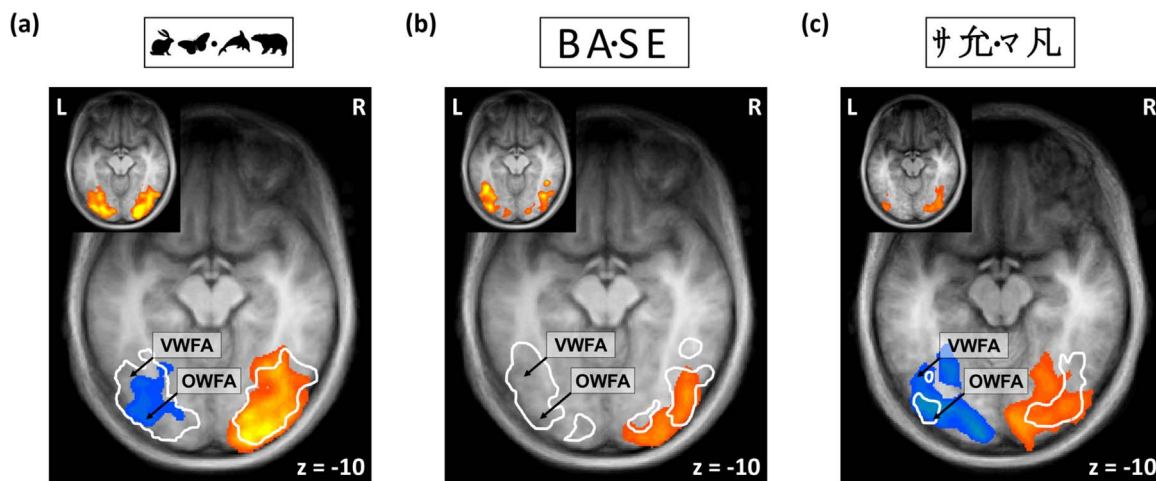
Fig. 3. Results of whole brain analysis from Experiment 1, Strother et al. (2016), and Experiment 3. The smaller scale brain shows activation in ventral occipitotemporal cortex (vOTC) yielded by the Different > Same contrast for each experiment, at q(FDR) < 0.05 (a) and (b), p < 0.005 uncorrected, (c). We observed repetition suppression in both the left and right vOTC for all three experiments. On the larger scale brain, the activation yielded by the RVF change > LVF change contrast is shown in blue and the LVF change > RVF Change contrast is shown in red. The thresholds are set at p < 0.01, uncorrected, for all three experiments. We observed there is no left hemisphere activation for RVF change > LVF change for Strother et al. (b), but the same contrast yield left vOTC activation for experiment 1 (a) and 2 (c). However, we observed that LVF change > RVF Change activated the right vOTC in all three experiments. White lines indicate regions showed repetition suppression observed from the smaller scale brain.

with the OWFA (but not the VWFA, at the chosen threshold), and was more pervasive in the right hemisphere than in the left.

In the reanalyzed data of Strother et al. (2016), contralateral bias was observed in the right hemisphere only, even at an extremely liberal threshold (*p* < 0.01, uncorrected; Fig. 3b). In the right hemisphere, the voxels showing a contralateral bias overlapped considerably with the repetition suppression results (white outlines in Fig. 3b). This indicates that contralateral bias throughout right vOTC, especially in areas showing repetition suppression, but a complete lack of contralateral bias in the left hemisphere (i.e., not restricted to the OWFA and VWFA), a result that was unique to the reanalyzed results of Strother et al.

In Experiment 2 (Fig. 3c), contralateral bias was again observed in both hemispheres, as in Experiment 1. In both hemispheres, this overlapped highly with the repetition suppression results (white outlines in Fig. 3c), and also overlapped with both the OWFA and VWFA, and was more pervasive in the right hemisphere than in the left. In short, the whole brain analysis of contralateral bias showed lack of contralateral bias in the left hemisphere only to word stimuli, which is consistent to the previous ROI analysis results.

To summarize, along with the results from the ROI analysis, we found different patterns of lateralization, both in terms of repetition suppression, and also contralateral bias for half-stimulus changes. In contrast to Experiments 1 and 2, repetition suppression in the reanalyzed results Strother et al.'s data showed left-lateralization of repetition suppression for word stimuli, and right lateralization with respect to contralateral bias (i.e., contralateral bias was uniformly weak in the left hemisphere, much more than in Experiments 1 and 2).

4. Discussion

Recent studies have reported left-lateralized involvement of occipital cortex in visual word form processing (e.g., Cohen et al., 2016; Yu et al., 2015), and Strother et al. (2016), proposed a specific function of neurons in this "occipital word form area" (OWFA) – to combine hemifield-split letters into a unified pre-lexical representation of visual word form. We performed two experiments and a reanalysis of a subset of Strother et al.'s data to study inter-hemifield integration of words as compared to nonverbal visual stimuli. Both experiments employed an fMRI repetition suppression technique used by Strother et al. to identify an occipital word form area (OWFA) in the left hemisphere, which integrates letterform information split between the right (RVF) and left (LVF) visual hemifields. Our study focused on the OWFA and the visual

word form area (VWFA) first reported by Cohen et al. (2000), as well as anatomically mirror-symmetric locations in the right hemisphere. The VWFA was initially characterized as a neural population that equivalently represents words presented to either the contralateral (RVF) or ipsilateral (LVF) visual hemifield (Cohen et al., 2002). In conjunction with other studies, this led to a model of visual word form processing in which hemifield-split letters are initially processed bilaterally in visual cortex, but eventually combined into a whole-word representation in the VWFA (Cohen et al., 2003). Our findings are consistent with this model but extend it to a more posterior anatomical locus in left occipital cortex, the OWFA. Crucially, we show that while both the OWFA and the VWFA participate in the inter-hemifield integration of visual input, this occurs to a lesser degree, if at all, for nonverbal stimuli. In addition to this main result, our experiments revealed interesting hemifield-hemisphere relationships in the visual processing of nonverbal visual stimuli.

In Experiment 1, in viewed strings of familiar animal silhouettes. Like words, these nonverbal stimuli were comprised of easily recognized two-dimensional shapes. However, unlike words, the animal silhouette strings formed no meaningful configuration. Our ROI analyses showed repetition suppression for repeated silhouette strings, and more importantly, consistently greater fMRI responses to contralateral versus ipsilateral half-string changes versus repetitions in all ROIs, including the OWFA and VWFA (i.e., both showed fMRI responses to *RVF change > LVF change*), which demonstrates greater contralateral versus ipsilateral visual hemifield sensitivity for nonverbal visual stimuli split between the RVF and LVF. While this result is consistent with heightened fMRI responses to whole objects viewed in the contralateral visual hemifield, even in anterior regions of visual cortex (Hemond et al., 2007; Sayres and Grill-Spector, 2008), it was not guaranteed given our stimuli and methods, which differed substantially from previous studies of contralateral bias in visual cortex. Our finding of contralateral bias for hemifield-split strings of silhouettes – which, like object images, elicit strong shape-related fMRI responses in visual cortex (Kourtzi and Kanwisher, 2001) – therefore extends previous findings of contralateral bias for objects viewed in isolation to those presented as part of a configuration viewed centrally. Additionally, a whole-brain analysis showed that overall repetition suppression was right-lateralized, consistent with other findings of right-lateralization during object recognition (Nakamura et al., 2005). A second whole brain analysis showed that the degree of contralateral bias was greater in the right hemisphere than in the left. While this may be related to an

asymmetry of visual attention between the RVF and LVF, especially in the context of serially presented visual stimuli (Matthews and Welch, 2015), no hemispheric asymmetries of contralateral bias were observed in the single-object studies mentioned earlier (Hemond et al., 2007; Sayres and Grill-Spector, 2008).

The main purpose of Experiment 1 was to compare the results to those obtained from the same participants in a previously published study. We therefore reanalyzed a subset of data (12 of the original 18 participants) from Strother et al. (2016), using new analyses, and we used the results of these analyses to perform direct comparisons with the results of Experiment 1. In terms of repetition suppression for whole strings – silhouettes in Experiment 1 and whole words in the published study – we observed some noteworthy differences between the two experiments. First, greater suppression in the right hemisphere than in the left (in whole-brain analyses), and the opposite pattern for words (which was evident in both ROI and whole-brain analyses). Left-lateralized repetition suppression for words was expected, but nevertheless validated our results with respect to known patterns of lateralization for words as compared to nonverbal stimuli.

Our comparison of primary interest was the degree to which fMRI responses in the OWFA and VWFA differed, or not, for the half-word change conditions (*LVF change* and *RVF change* conditions, in which letters in one hemifield changed but repeated in the other). In contrast to the contralateral bias observed Experiment 1, such that left hemisphere ROIs (OWFA and VWFA) showed greater responses to RVF half-word changes, and vice versa for the right hemisphere ROIs (OFA and rVWFA), neither the OWFA nor the VWFA showed any difference in fMRI responses to contralateral versus ipsilateral half-word changes. This was not true of either the OFA or the rVWFA, both of which showed heightened fMRI responses to contralateral half-word changes. This result is consistent with the results Strother et al. (2016), and it is also a novel reanalysis of data from a subset of their participants, which was necessary for direct comparison with Experiment 1 (in which data were collected from the same participants). In short, the results of our reanalysis of published data and direct comparison with the results of Experiment 1 show that equivalent sensitivity of the OWFA and VWFA to half-word changes, irrespective of hemifield, is not necessarily observed for nonverbal stimuli, a prediction we tested further in Experiment 2.

The lack of contralateral bias for half-word changes in the OWFA and VWFA was further substantiated by a whole-brain comparison of fMRI responses in the *LVF change* and *RVF change* conditions for words as compared to silhouette strings—indeed, in contrast to the whole-brain analysis results for Experiment 1, no significant differences in fMRI responses between the two half-word change conditions were observed in the entire left hemisphere (in a group level RFX analysis). This means that, contralateral bias for half-word changes is relatively weak in the left hemisphere as compared to the right hemisphere, and that the OWFA and VWFA show concomitant maximal repetition suppression to words and minimal or non-existent contralateral bias for half-word changes, despite contralateral bias for half-stimulus changes in Experiment 1. While this result is consistent with the predictions of some existing models of word recognition (Cohen et al., 2003; Molko et al., 2002), these models predict our VWFA results only, not the word-specific lack of contralateral bias in the OWFA. Our results also highlight the relationship between our results and our method – in contrast to presenting whole words or whole objects to either the RVF or LVF (e.g., Cohen et al., 2002; Hemond et al., 2007; Niemeier et al., 2005; Rauschecker et al., 2012; Sayres and Grill-Spector, 2008), we used a novel half-field fMRI method applied to words and nonverbal strings. A possible criticism is that our word stimuli were artificially large, which could be worth studying in future experiments.

A limitation of our comparison of the Experiment 1 results is that our choice of nonverbal stimuli were definitively nonverbal. That is, none of our participants would have mistaken them for linguistic stimuli. In Experiment 2 we therefore used Japanese character string stimuli that were recognized as linguistic but processed as nonverbal stimuli because all of our participants were monolingual English readers. Experiment 2 served three main purposes. First, it involved a new set of participants. Second, the stimuli were more closely matched in spatial frequency to those used in our previous study with words, but nevertheless elicited right-lateralized repetition suppression (as in Experiment 1). This is extremely important given known hemispheric differences in sensitivity to high versus low spatial frequencies (e.g., Roberts et al., 2013; Woodhead et al., 2011). Third, and more importantly, the results of Experiment 2 replicated the results of Experiment 1 with respect to contralateral bias for half-stimulus changes, which was observed in all ROIs (both hemispheres) and also in a whole-brain analysis. That is, the only evidence of equivalent fMRI responses to contralateral and ipsilateral half-stimulus changes was observed for words, in the OWFA and the VWFA, further evidence that neurons in these areas are involved in visual processing that is unique to word recognition.

We interpret the results of our experiments, and the comparison of these results of a subset of previously published data analyzed using different methods, as evidence of word-specific hemifield integration in the OWFA and VWFA. While the VWFA result is consistent with existing models and experimental findings (Cohen et al., 2003; Molko et al., 2002), including finding from fMRI repetition suppression (Glezer et al., 2009), our observation of the same effect in the OWFA suggests that inter-hemifield integration of word form information occurs outside of the VWFA, and possibly during an earlier pre-lexical stage of shape processing than predicted by existing models of whole-word representation in the visual system. Interestingly, a similar proposal has been offered recently to explain right-lateralized face processing (Frässle et al., 2016), which exhibits striking parallels with word recognition (Behrmann and Plaut, 2013; Dehaene et al., 2015; Dundas et al., 2012), especially with respect to symmetry processing (Bona et al., 2015; Kietzmann et al., 2015), which may have a parallel in the OWFA for "symmetry breaking" in visual word form processing (possibly in addition to the VWFA; Pegado et al., 2011). Furthermore, given that defective callosal transfer and inter-hemispheric coordination is associated with dyslexia (Fabbro et al., 2001; Henderson et al., 2007), our findings highlight the possibility that at least some cases of dyslexia may be the result of impaired inter-hemifield integration (Kelly et al., 2004).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.neuropsychologia.2017.04.003.

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