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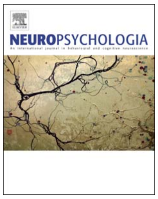

An fMRI study of visual hemifield integration and cerebral lateralization

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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

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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 contralateral and ipsilateral hemifield-specific repetition suppression or release 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; $2 \times 2 \times 2\ \text{mm}^3$ 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

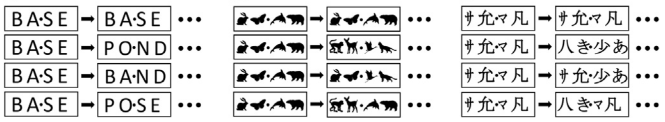

Fig. 1. Stimuli and conditions used in Strother et al. (2016) and Experiments 1 and 2: (a) words; (b) silhouettes; and (c) Japanese character strings. The top row shows paired examples of Same (repeated) stimuli. The second row shows examples of Different (non-repeating) stimuli. The third and bottom 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).