



Special issue: Research report

Left hemisphere specialization for word reading potentially causes, rather than results from, a left lateralized bias for high spatial frequency visual information

Alexandra Ossowski and Marlene Behrmann*

Department of Psychology, Center for the Neural Basis of Cognition, Carnegie Mellon University, Pittsburgh, PA, USA

ARTICLE INFO

Article history:

Received 6 September 2014
 Reviewed 2 November 2014
 Revised 1 December 2014
 Accepted 5 December 2014
 Published online 7 January 2015

Keywords:

Hemispheric lateralization
 Development
 Reading
 Spatial frequency
 Cortical organization

ABSTRACT

There is considerable evidence showing that efficient visual word recognition relies on high spatial frequency (HSF) visual coding in the left posterior fusiform gyrus. But whether the bias for HSF in the left hemisphere (LH) causally contributes to the LH superiority for word recognition or possibly results from it remains unknown. To assess whether the lateralization for HSF information exists prior to the left lateralization for reading, we used a divided-visual field task to examine the LH bias for orthographic processing and for HSF Gabor patches in young children (mean age 4.5 years) with variable letter knowledge, and in adults. If LH specialization for orthographic processing results from a pre-existing HSF bias in the LH, then LH specialization for HSF information should be evident even in those young children with minimal, if any, letter knowledge. The adult participants showed the predicted LH lateralization for both HSF information and word recognition. Neither of these hemispheric biases, however, was statistically significant in the group of young children. Further investigation, however, revealed a correlation between these biases such that those children with the somewhat more developed LH advantage for orthographic representations also evinced an LH bias for HSF information. These findings suggest that, rather than serving as a precursor for the LH superiority for word recognition, the LH bias for HSF input might emerge in concert with it or potentially even be a consequence of the acquisition of orthographic competence.

© 2015 Elsevier Ltd. All rights reserved.

1. Introduction

It is well established that, in most right-handed individuals, the left hemisphere (LH) plays a much greater role in reading

and word recognition than the right hemisphere (RH). Several decades of research support this claim including evidence from neuropsychological case studies, electrophysiological (ERP) recordings, and neuroimaging data. For example, a

* Corresponding author. Department of Psychology, Carnegie Mellon University, Pittsburgh, PA 15213-3890, USA.

E-mail address: behrmann@cmu.edu (M. Behrmann).

<http://dx.doi.org/10.1016/j.cortex.2014.12.013>

0010-9452/© 2015 Elsevier Ltd. All rights reserved.

lesion to the left occipitotemporal cortex gives rise to pure alexia [for review, see (Behrmann, Plaut, & Nelson, 1998)] and, although BOLD activation in response to words is evident bilaterally, there is stronger and more robust activation of the LH (visual word form area, VWFA) than of the RH [for recent example, see (Woodhead, Wise, Sereno, & Leech, 2011)]. Consistent with this, ERP recordings have consistently shown that in adults, the standard electrophysiological marker for pattern recognition, the N170, is significantly left lateralized for words as compared to other stimuli, such as faces and symbol strings (Mercure, Dick, Halit, Kaufman, & Johnson, 2008; Rossion, Joyce, Cottrell, & Tarr, 2003).

The LH lateralization for word recognition seems to emerge over the course of development as letter identification is gradually acquired. Behavioral studies have documented an emerging right visual field/LH advantage for letters in a divided-visual field task, as children develop the ability to name letters (Davidoff & Done, 1984; Jablonowska & Budhoska, 1976). Consistent with this, the left-lateralized N170 is absent in children who have not yet acquired letter knowledge, and the N170 increases in amplitude as children develop letter knowledge (Dundas, Plaut, & Behrmann, 2014; Maurer, Brem, Bucher, & Brandeis, 2005). Cross-sectional developmental fMRI studies have also found an increased leftward asymmetry related to increases in age and linguistic skill as well as to the acquisition of word recognition (Schlaggar et al., 2002; Schlaggar & McCandliss, 2007; Turkeltaub, Gareau, Flowers, Zeffiro, & Eden, 2003).

1.1. The contribution of spatial frequency bias to LH word lateralization

As is evident, there is considerable support for the claim that the LH is tuned for representations of orthographic stimuli and that this organization emerges and is enhanced over the course of development. The key question is what drives the LH (rather than the RH) to become specialized for word recognition. One obvious explanation is that it is the LH dominance for language, present in the majority of the population, that biases the tuning for word recognition (Bouhali et al., 2014; Cai, Paulignan, Brysbaert, Ibarrola, & Nazir, 2010; Dundas, Plaut, & Behrmann, 2013) and that the top-down pressure from language areas likely play a critical role in configuring the LH VWFA (Price & Devlin, 2011). The question is whether this linguistic bias or pressure suffices as the explanation for the left lateralization of word processing, or whether there might also be an inherent low-level or sensory bias in the visual system that predisposes the LH to the acquisition of word recognition.

With regard to the latter, one possibility is that the left lateralization for reading may be an outgrowth of an evolutionarily older specialization of the LH at the basic sensory level, namely the ability to detect fine edges and sudden changes in visual space, referred to as high spatial frequency (HSF) visual information (Ivry & Robertson, 1998; Sergent, 1982; Sergent & Hellige, 1986). Spatial frequency refers to the number of contrasting light/dark (luminance) cycles per unit space (for example, per one degree visual angle). Sudden and frequent changes in a given area of space constitute fine edges, or HSF, whereas coarse changes over large distances

reflect low spatial frequency information in the image. The detection of fine edges constituting HSF is necessary for discriminating individual letters so that words can be accurately read. Therefore, any pre-existing LH bias for HSF visual input may contribute to the emergence of the LH lateralization for word reading.

Converging evidence has confirmed the differential sensitivity of the two hemispheres to different spatial frequencies in the visual input, with the LH more biased to processing HSF and the RH to LSF information [for review see (Tadros, Dupuis-Roy, Fiset, Arguin, & Gosselin, 2013)]. Additional evidence for LH tuning for HSF comes from imaging studies showing significant leftward lateralization in the posterior occipitotemporal region for images and gratings closer to 7 cycles per degree, and increased RH activation for images and gratings closer to .5 cycles per degree (Seghier & Price, 2011; Woodhead et al., 2011). This differential preference for HSF versus LSF visual information is particularly pronounced in the left and right fusiform gyri (Woodhead et al., 2011) but is also observed in other areas of cortex. For example, Fintzi and Mahon (2014) reported that the left orbitofrontal cortex accesses HSF visual information in its contribution to object recognition, whereas the right orbitofrontal cortex's contribution to object recognition is primarily based on the LSF information. Additionally, behavioral studies (Peyrin, Chauvin, Chokron, & Marendaz, 2003; Sergent, 1982) and case studies of patients with LH versus RH brain damage (Ivry & Robertson, 1998) have demonstrated an increased sensitivity to HSF in the LH, and an increased sensitivity to LSF in the RH. Mercure et al. (2008) also observed that HSF input was associated with increased leftward lateralization of the N170 ERP for word recognition. Last, in a large case-series of patients with lesions centered on left posterior fusiform gyrus, there was both reduced sensitivity to HSF concomitant with prolonged response latencies both in reading (pure alexia) and object naming (Roberts et al., 2012).

Beyond a relative bias favoring HSF in the LH, the LH appears to be tuned to particular HSFs that are appropriate for deciphering text. Consistent with functional imaging studies noted above, Kitterle, Christman, and Hellige (1990) used a divided-visual field paradigm, in which HSF and LSF gratings were presented to the right visual field (RVF) or the left visual field (LVF), and then measured the spatial frequency tuning of the two hemispheres. Participants were faster at identifying gratings in the range of 6–9 cycles per degree in the RVF/LH, and faster at identifying gratings in the range of .5–2 cycles per degree in the LVF/RH. Given that a letter can be accurately identified based on a spatial frequency band from 1.5 to 10 cycles per letter (Majaj, Pelli, Kurshan, & Palomares, 2002), the results of this half-field study are consistent with the claim that letter perception is well suited to LH visual computation.

As a means of exploring the role of spatial frequency in the visual computations of the two hemispheres, Hsiao and Cottrell (2009) proposed that because many letters are shared in English words, accurate recognition requires the reader to discern the identity of each letter (such as the middle letter of “hot” vs “hat”) and this implicates the processing of HSF information. To examine this hypothesis in detail, Hsiao and colleagues (Hsiao & Lam, 2013; Hsiao, Shieh, & Cottrell, 2008) have explored hemispheric neural network models in

which the LH was biased towards higher spatial frequencies than the RH, and have shown that this differential sensitivity caused the LH to play a greater role in learning to recognize words. These models clearly adopt the assumption that HSF is the key characteristic that gives rise to the lateralization of letter and word perception. In subsequent research, to elucidate the anatomical properties of the LH that potentially drives the word lateralization, [Hsiao, Cipollini, and Cottrell \(2013\)](#) argued that the differential connectivity patterns of the two hemispheres might give rise to the differential frequency processing. The differential anatomical connectivity was implemented in a neural network model which accounted for a host of empirical findings, including the asymmetry in global (more RH) and local (more LH) perception, leading the authors to conclude that it is specifically the hemispheric asymmetry in connection structure that causes both the HSF tuning and the word lateralization. Regardless of whether the hemispheric differences in spatial frequency sensitivity arise from intrinsic differences in connectivity structure or from some other fundamental bias, the question to be addressed here remains the same – does the apparently fundamental LH advantage in processing HSF information give rise to the left lateralization of orthographic representation?

1.2. Developmental emergence of letter and word perception: a causal account

Thus far, we have discussed two factors that might contribute to the LH dominance for letter and word perception that is evident in adulthood and that emerges over the course of development: 1) the LH bias for language, and 2) the differential bias of the LH for HSF information. In the current study, we assess this second factor by examining the relationship between the LH HSF bias and orthographic proficiency. If the spatial frequency bias of the LH plays a causal role in the lateralization of reading to the LH, then LH sensitivity to HSF information should be in place before LH specialization for reading occurs. If, however, there is no LH HSF bias in advance of orthographic skill, then there are two possibilities: either the HSF and the word bias emerge in tandem or the causality may even be reversed, with the LH HSF bias being a result of reading acquisition (for similar approach testing precursors of reading in pre-reading children but focused on neuroimaging, see [Clark et al., 2014](#)). Contrast sensitivity to HSF information reaches adult levels near the age of 4 years ([Adams & Courage, 2002](#)), presumably before left lateralization for reading ability is thought to occur and so lateralization for HSF in the LH may potentially be in place before reading is acquired. However, because no data exist regarding the specific HSF sensitivity in the LH, nor the relationship between HSF and reading ability, this issue remains unresolved.

1.3. The current study

To determine whether the LH bias for HSF precedes reading acquisition, we examined the hemispheric lateralization patterns for orthographic processing and spatial frequency sensitivities in young children aged 4–5 years of age and in adults. Words (or letters for the young age group) were presented to each visual field, with the expectation that, as in

previous studies, the adults, but not the young children, would show a greater degree of LH lateralization for identification of letters/words. Critically, to determine whether the LH bias for HSF precedes word recognition (and its lateralization) developmentally, we measured sensitivity to HSF and LSF in both visual fields. Here too, we expected that adults would show a clear LH HSF bias. If HSF bias is present prior to word/letter reading, then the young children should also show an LH HSF bias and this should be evident even in those children with minimal, if any, letter recognition skills.

2. Experimental methods

2.1. Participants

The study was approved by the Carnegie Mellon Institutional Review Board and by the administrators of the Carnegie Mellon Children's School. All participants (or their legal guardians) gave informed consent.

Children: Fifteen children, mean age of 4.5 years ($SD = .52$), 8 male and 7 female, and all with normal or corrected-to-normal vision, were recruited from the Carnegie Mellon Children's School. Children with a history of visual, developmental, or neurological disabilities were excluded from the study, and all children were right-handed as established by teacher report.

Adults: A group of 15 undergraduate students at Carnegie Mellon University (9 females, 6 males), aged 19.8 years ($SD 2.4$ years) participated in the study. Participants received \$10 or course credit as compensation, and testing took a maximum of 1 h in duration. All adult participants were right-handed ([Oldfield, 1971](#)), native readers of English, had no history of visual or neurological problems, and had no history of reading difficulties. The mean handedness score of the group was 74.1 ($SD 8.9$).

2.2. Stimuli

Two Gabor patches, one of 1.5 cycles per degree and one of 6 cycles per degree, in both the vertical and horizontal orientation, were generated using MATLAB software (MathWorks, 2012). The patches were 1.5 inches in height \times 1 inch in width, and 130×130 pixels. For the adult participants, the patches were presented at a contrast level of .3, but this level was increased to .4 for the children. This latter parameter was determined based on pilot data, in which we established that a .4 contrast level was necessary in order for the children to achieve an accuracy level above 70%. The screen resolution of the laptop on which these patches appeared was 1366×768 . The Gabor stimuli appeared against a black background (see [Fig. 1](#)).

The word stimuli, taken from a prior experiment ([Dundas et al., 2013](#)), consisted of 60 four-letter words shown in gray Arial 18 point font against a black background. The words were approximately $\frac{1}{2}$ inch in height and 1 inch in width. Pairs of words were constructed so that words would differ by one of their interior letters in order for a same/different task to be performed, for example 'bead' and 'bend' (see [Fig. 2a](#)).

Uppercase letter stimuli used in the children's task were in gray Arial 18 point font, and appeared against a black

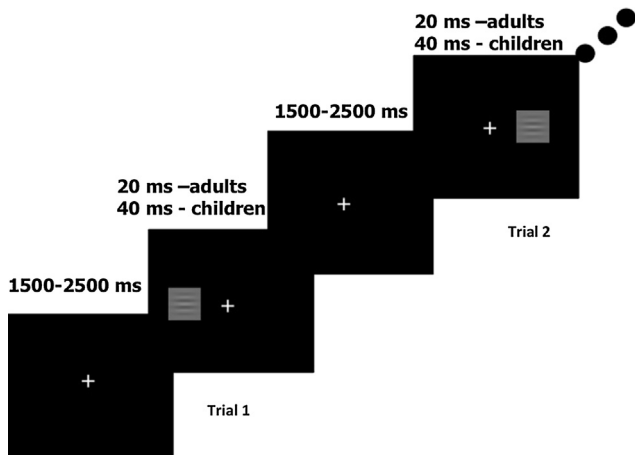


Fig. 1 – Example of a sequence of two trials in the hemifield spatial frequency task. Following a central fixation, a Gabor stimulus was presented briefly to the left or right visual field and participants decided if the stimulus had wide or narrow stripes. After another fixation screen, the next Gabor stimulus was then presented to the left or right visual field. The sequence continued until the experiment was completed.

background. The letters were approximately $\frac{1}{2}$ inch in height and in width. Thirteen commonly used letters, according to the Oxford English Dictionary, were used as stimuli in the experiment (E, A, R, I, O, T, N, S, L, C, U, D, P) (see Fig. 2b).

2.3. Experimental procedure

The experiment was run on a laptop using E-Prime software, version 2.0 (Schneider, Eschman, & Zuccolotto, 2002). Participants were seated approximately 15 inches from the screen and, for adults, a chinrest was used to limit head movements. Testing took place in a quiet room with the lights dimmed, and participants were instructed to look directly at the center of the computer screen.

The spatial frequency identification task was similar to the paradigm used by Kitterle et al. (1990) and employed a 2×2 design (high/low spatial frequency \times right/left visual field; see Fig. 1). On each trial, following a fixation screen in which a cross appeared directly in the center of the screen (jittered between 1500 and 2500 msec to reduce anticipatory responses), a single Gabor patch appeared briefly in the RVF or LVF, and participants were required to make a two-alternative forced choice response as to whether the stimulus had wide (LSF) or narrow (HSF) stripes. The center of the lateralized stimulus was 5.3° from fixation. Participants responded via button press using the “H” and “G” keys on the keyboard and the stimulus-response arrangement was counterbalanced across participants. The HSF and LSF stimuli appeared an equal number of times in each field. For adults, the Gabor patch appeared for 20 msec (Fig. 1), whereas for the children, the patch appeared for 40 msec, a parameter determined through pilot testing. Following response, the fixation screen re-appeared (again jittered for 1500–2500 msec). The brief exposure duration precluded saccades and encouraged the

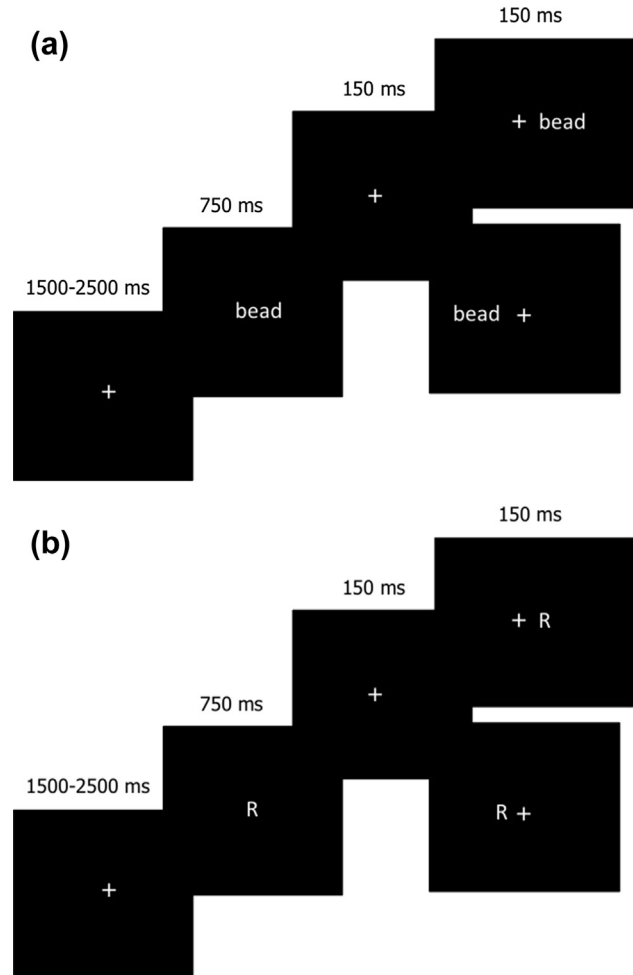


Fig. 2 – Example of a sequence of trials appearing in the hemifield word task. (a) Adults. Following a fixation screen, a four-letter word appeared centrally. It was replaced by a brief fixation and thereafter a second word was shown in the left or right visual field for same/different discrimination. (b) Children. Following a fixation screen, a single letter appeared centrally. It was replaced by a brief fixation and thereafter a second letter was shown in the left or right visual field for same/different discrimination.

maintenance of central fixation. Adults performed 96 trials of the spatial frequency task, took a short break, and performed another 96 trials, for a total of 192 trials. The children performed the task for as long as they were willing; the mean number of trial was 89 (SD 15.3). Participants were encouraged to maintain fixation throughout and to respond as quickly and as accurately as possible.

In the divided-field word task for adults, on each trial, following a fixation screen (jittered between 1500 and 2500 msec to reduce anticipatory responses), a single word appeared in the center of the screen for 750 msec, after which a brief fixation (150 msec) was presented (see Fig. 2a for an example of a trial and the associated timing). Immediately thereafter, a second word appeared to the right or left of fixation for 150 msec. The center of the lateralized word was 5.3° from fixation. The second word either matched or did not match the

word presented in the center. Participants again made a two-alternative forced choice judgment using the “G” or “H” keys on the keyboard, with the stimulus-response mapping counterbalanced across participants. Adults performed 96 trials of this task, took a short break, and performed another 96 trials, for a total of 192 trials. The children performed a variant of this task in which, instead of words, a single letter was presented for same/different discrimination using the identical timing and parameters as for the word task (see Fig. 2b). Children completed as many trials as they were willing to do; the mean number of trials was 91.7 (SD 9.7). As for the previous task, participants were encouraged to maintain fixation and to respond as quickly and as accurately as possible.

Each child participant completed four sessions for up to 20 min each, or until the child requested to stop. One session consisted of a practice version of the spatial frequency task, so that the child could become accustomed to using the computer and responding via key press. Each child then completed one session of the divided-visual spatial frequency task, one of the divided-visual letter identification task, and one involving the assessment of reading abilities (see below). Adult participants all completed the divided-visual field spatial frequency discrimination task and the divided-field word same/different task in a single session. The order in which the two tasks were presented was counterbalanced across participants in each of the two age groups (adults or children).

Finally, the child participants completed the CORE Phonics Survey (Diamond & Thorses, 2008), which is a brief assessment of reading ability and letter knowledge, and provided an estimate of the reading capabilities of each participant. This survey consists of three sections run in the following order: letter identification, phoneme identification and word identification. In the letter identification section, the children were shown 26 uppercase and lowercase letters individually and the child responded whether s/he knew what letter it was and then reported it out loud. For the phoneme identification, the child was shown the same letters and asked if s/he knew ‘what sound the letter made’ and the child responded verbally with the sound. In the letter and phoneme identification subtests, if a child could not name three consecutive letters/phonemes, the experimenter instructed the child to look at each remaining letter and name the ones s/he did know, before moving on to the next subtest. Finally, the children were shown 7 sets consisting of 10 real words and 5 pseudowords. The experimenter pointed to individual words and asked the child if s/he knew what the word was. If a child could not name 2 consecutive words in one of the sets, the experimenter moved on to the next set. For our purposes, responses were recorded for the child’s accuracy in each section, in order to generate a separate score for letter identification, phoneme identification, and word recognition. A composite score (sum of scores for all three sections) was also calculated. These scores were then correlated with performance on the divided-field spatial frequency and word/letter discrimination tasks.

3. Results

We first report the lateralization of spatial frequency responses and of word perception in adults to ensure that our

paradigms successfully elicit the expected patterns of LH superiority for both HSF and word matching. We then examine the lateralization profiles of the children for the two tasks, as well as the correlation between their performance on each task and the correlations between the two experimental tasks and the CORE literacy measures.

3.1. Left lateralization for HSF Gabor patches in adults

As in the experiments of Kitterle et al. (1990), accuracy for reporting high versus low spatial frequency was extremely high and over 95% in most cases (see Fig. 3a). Therefore, it was not possible to conduct any statistical analyses of hemispheric differences/visual field preferences using accuracy as a dependent measure. Using reaction time (RT) as the dependent measure, and spatial frequency (HSF/LSF) and visual field (left/right) as within-subject factors, we observed a marginally significant interaction between spatial frequency and visual field [$F(1, 14) = 3.43, p = .08$] (see Fig. 3b). Pairwise *t*-tests reveal no statistically significant RT advantage for HSF over LSF patches in the LVF (RH) (HSF vs LSF: 586 msec vs 590 msec; n.s.) but a statistically significant 33.3 msec RT advantage for HSF over LSF patches in the RVF (LH) (HSF vs LSF: 561.6 vs 594.9 msec; [$t(1,14) = 7.1, p < .02$]). There was also a significant difference in HSF RTs across the two fields [$t(1,14) = 4.4, p = .05$]. These findings attest to the HSF bias in the RVF/LH, as predicted. No other effects were significant.

The clearer RVF/LH advantage for HSF visual information without a corresponding LVF/RH advantage for LSF visual information is perhaps perplexing but is consistent with data from Kitterle et al. (1990), where the LH advantage for HSF visual information was more salient and easier to detect than the RH advantage for LSF visual information. This result also replicates the LH advantage for stimuli of over 1.5 cycles per degree for the LH but no clear advantage for any spatial frequencies in the RH (Proverbio, Zani, & Avella, 2002). While this discrepancy across the two fields may be worth exploring more generally, for the current purposes, the presence of the RVF/LH advantage for HSF Gabor patches is sufficient to enable us to examine our key hypotheses concerning the relationship of HSF and orthographic processing.

3.2. Left lateralization for words in adults

To assess the lateralized processing of words, we examined both RT and accuracy differences for word matching in the two visual fields (see Fig. 4). A one-way ANOVA on accuracy as the dependent measure revealed a small but significant advantage for the RVF/LH (89%) over the LVF/RH (85%), [$F(1,14) = 7.4, p = .017$] (Fig. 4a). The same analysis conducted with RT also revealed a significant difference across fields, [$F(1, 14) = 10.2, p = .006$], with a 42.3 msec RT advantage for words in the RVF over the LVF (means RVF vs LVF: 678.9 msec vs 721.2 msec) (Fig. 4b).

3.3. Left lateralization for HSF Gabor patches in children

The findings from the adult participants confirm the bias for processing HSF information in the LH and also support the well-established pattern of an advantage for word processing

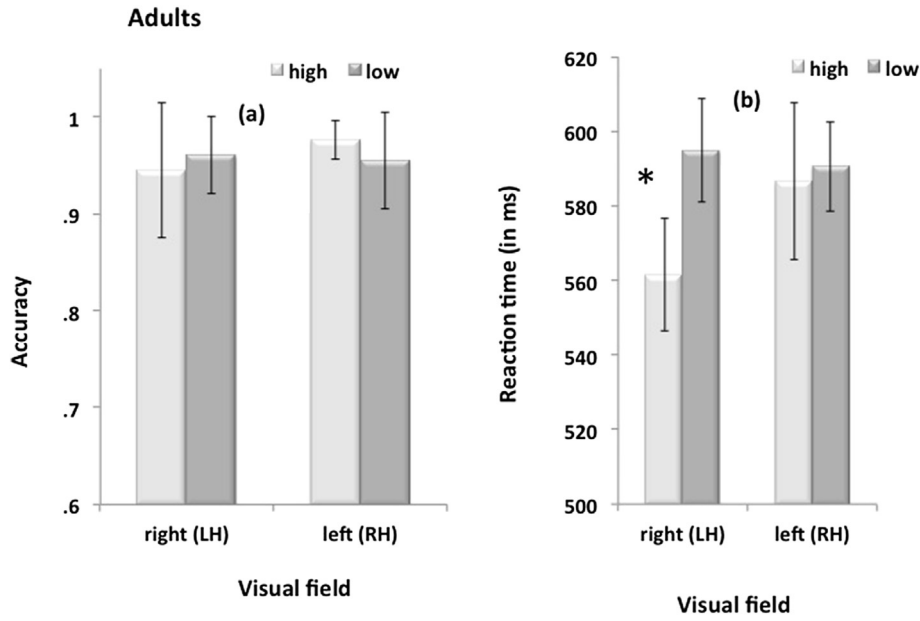


Fig. 3 – Mean (a) accuracy and (b) reaction times (RT) for high and low spatial frequency Gabor patches in the right and left visual fields. Accuracy rates are close to ceiling. RT for high spatial frequency Gabor patches are significantly faster in the right visual field, while RT for low spatial frequency Gabor patches are moderately faster in the left than in the visual field. Significant differences are indicated by (*).

in the LH. Having replicated the expected pattern of LH lateralization, and confirmed that these paradigms have sufficient sensitivity to uncover the effects of interest, we now evaluate whether young children evince the LH HSF bias and the LH word orthography advantage (noting that we used letters rather than words to assess hemispheric superiority for orthographic material in the children).

A repeated measures ANOVA with visual field (left, right) and spatial frequency (high or low) as within-subject factors and accuracy as the dependent measure yielded neither a main effect of visual field, [$F(1,14) = 1.1, p > .3$] nor an

interaction of visual field \times spatial frequency, [$F(1,14) = .021, p > .5$] (see Fig. 5a). There was, however, a significant main effect of spatial frequency, [$F(1,14) = 33.5, p < .001$], with higher accuracy (mean = .90) for LSF than HSF patches (mean = .81). In the same analysis but using RT (see Fig. 5b), no main effects reached significance [visual field ($F(1, 14) = 1.27, p > .2$; spatial frequency ($F(1,14) = 1.8, p > .1$)] and the interaction between these two factors did not reach significance ($F(1, 14) = .33, p > .5$).

Because the pattern of differences between HSF and LSF patches in the right and left visual fields were somewhat

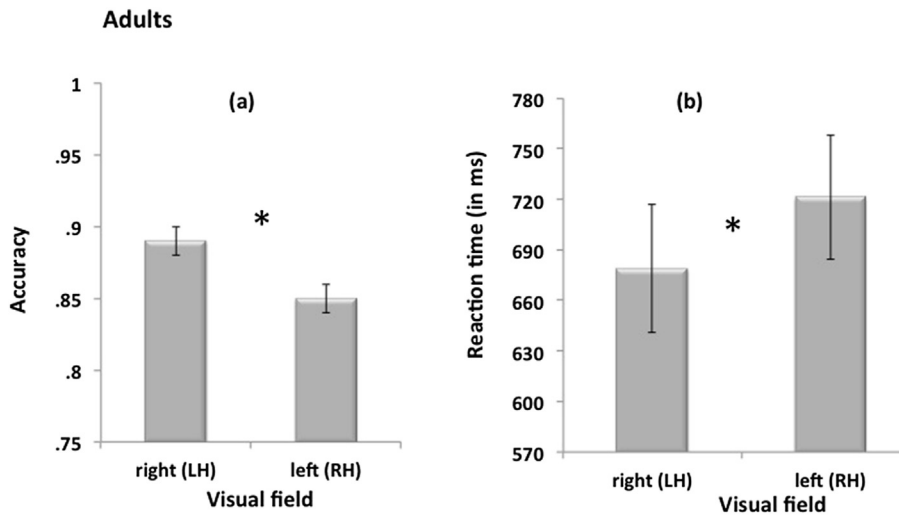


Fig. 4 – (a) Mean percent accuracy for words appearing in the left and right visual fields with significantly higher accuracy for words in the right visual field/left hemisphere than for words appearing in the left visual field/right hemisphere. (b) Mean RT for words in the left and right visual fields with significantly faster performance in the right visual field/left hemisphere than in the left visual field/right hemisphere. Significant differences are indicated by (*).

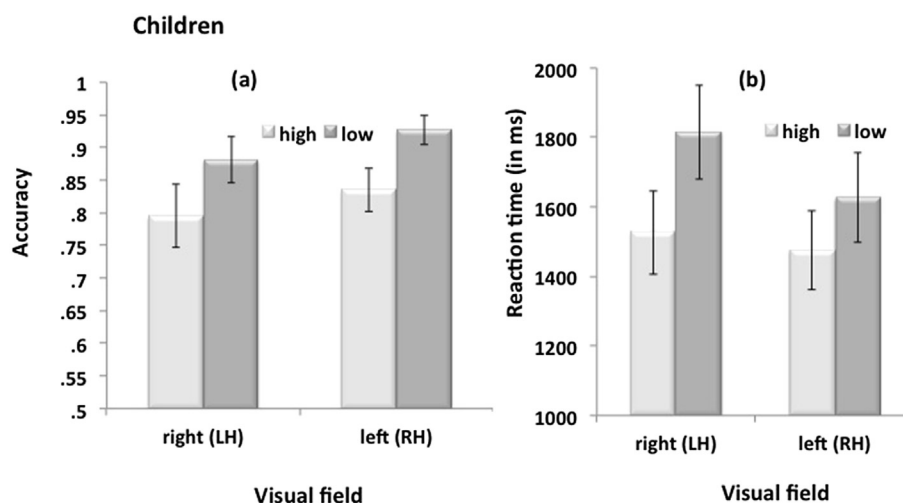


Fig. 5 – Children data. (a) Mean percent accuracy for high and low spatial frequency Gabor patches in the right and left visual fields. Accuracy for high and low spatial frequency Gabor patches is not significantly different between the left and right visual fields. (b) Mean reaction times (RT) for high and low spatial frequency Gabor Patches in the right and left visual fields. RTs for high and low spatial frequency Gabor patches are not significantly different between the left and right visual fields.

different for RT and for accuracy (Fig. 5a, b), we explored whether young children demonstrated a speed/accuracy tradeoff, with lower accuracy on trials in which their responses were faster. To adjust for this possible tradeoff, we computed the inverse efficiency (IE) scores (RT/Percent Correct) (Townsend & Ashby, 1983) for each child participant for HSF and LSF Gabor patches in each visual field. A repeated measures ANOVA (visual field \times spatial frequency) using the IE scores yielded no significant effects of either factor [visual field ($F_{1,14} = .29, p > .5$); spatial frequency ($F_{1,14} = 2.3, p > .05$); and no interaction between them ($F_{1,14} = .56, p > .3$)] confirming the absence of differential sensitivities for HSF and LSF in either visual field.

The null results for visual field and frequency in the data from the children is unlikely to result from a lack of power. First, we have the same number of participants in the child and adult group, but find statistical effects only in the latter. Second, we do see a main effect of frequency in the accuracy data within the children's group suggesting that power is not obviously limited. Although adults' accuracy was very close to ceiling and the effects emerged in RT whereas the task appears to be data-limited in the children and the results (that exist) are more evident in accuracy than in RT, we nevertheless compared the adults versus children using IE as the dependent measure and visual field and frequency as within-subject variables. Unsurprisingly, there was a significant main effect of group, [$F_{1,28} = 39.5, p < .001$], with higher IE measures (indicating poorer performance) in the children than in the adults. There was also a marginally significant main effect of frequency, [$F_{1,28} = 3.4, p = .06$], favoring HSF information. There was only a rough trend towards a frequency \times visual field \times group interaction, [$F_{1,28} = .93, p = .2$] and this is presumably a result of the fact that some subset of the children (see below) do show an LH HSF bias but that at a group level, because of the variability amongst the children, this bias is not statistically significant.

3.4. Left lateralization for letters in children

The next analysis explored the presence of a hemispheric advantage for letter processing in the young children. A one-way ANOVA (left vs right visual field) yielded no significant difference in letter matching accuracy ($p > .3$) (Fig. 6a) nor in RT ($p > .4$) (Fig. 6b). As with the analysis of HSF versus LSF information in the different visual fields, we computed the IE scores for letter matching in the left and right visual fields. A one-way ANOVA using IE scores for letters appearing in the left and right hemispheres also yielded no significant effects ($p > .05$).

One potential reason for the absence of a hemispheric difference in the young children might have to do with the fact that the letter matching measure we used was insufficiently sensitive as an index of orthographic knowledge. Although we elected not to use the adult word matching task and modified the task to be more appropriate for the young children, it remains possible that we did not design a measure that could uncover any existing hemispheric differences. Therefore, to evaluate whether the letter matching task accurately captured the reading abilities of the children, we correlated the children's letter matching performance on the divided-field task with their scores on the letter reading section of the standardized Core Phonics Survey (see Methods for details). To do so, we conducted Pearson correlations between RT, accuracy and IE for letter matching in the right and left visual fields with the results of the letter section of the Phonics Survey. More specifically, for each child, as a measure of assessing reading competence in the RVF/LH, which is the metric of interest, we calculated the difference in dependent measure between the LVF and the RVF and the Pearson correlations were performed using these difference scores.

This analysis revealed a significant correlation between RT for letters presented to the RVF/LH and letter knowledge as measured by the letter identification scores on the CORE Phonics Survey ($p = .004$, Fig. 7), with better CORE Phonics letter score associated with faster RT. The same result was

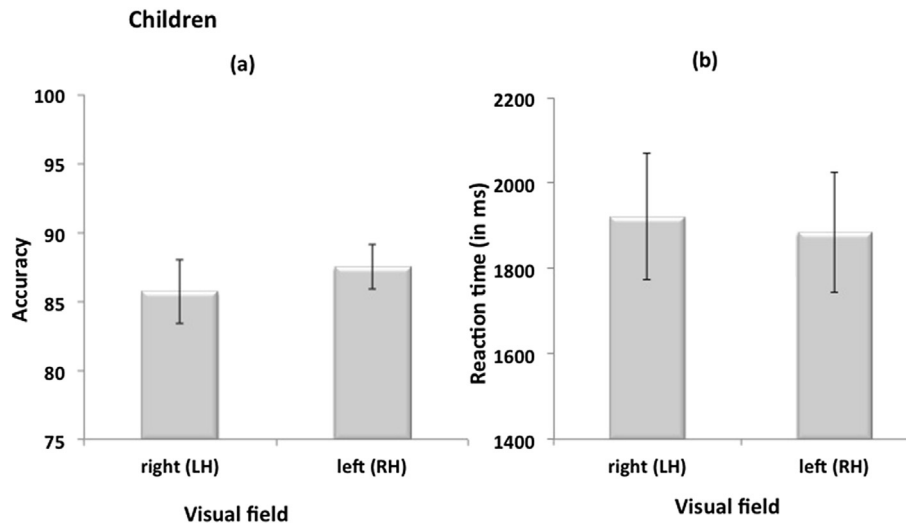


Fig. 6 – Children data. (a) Mean percent accuracy for letters in the left and right visual fields. No significant difference in RT between the left and right visual field occurred. (b) Mean reaction times (RT) for letters in the left and right visual fields. No significant difference in RT between the left and right visual field occurred.

obtained between the RT for letters computed in IE for letter matching in RVF/LH and the score for letters on the CORE Phonics Survey ($r = -.607, p = .016$). We also explored whether this correlation was specific to the RT for the RVF/LH by examining the correlations between the RT for letters in the LVF/RH and the score for letters on the CORE Phonics Survey. Thus, we conclude that better performance in the LH than RH in letter matching is a reliable reflection of letter reading ability as measured by the independent, standardized CORE test. This finding suggests that the absence of a difference in hemispheric processing of letter matching in children is not obviously a result of insensitivity of the measure used.

3.5. Direct comparison of lateralization between children and adults

Although the testing paradigms differed between adults and children, we still attempted to compare the groups in terms of

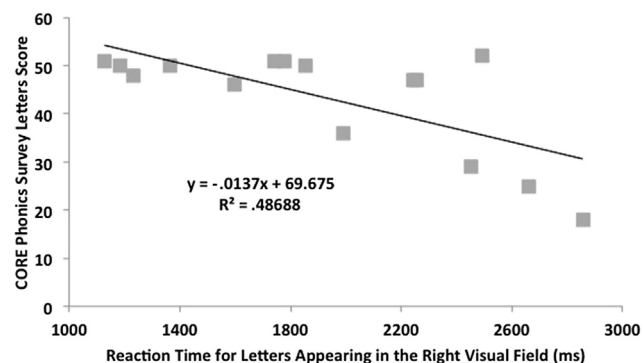


Fig. 7 – Children data. Reaction time for letter discrimination in the RVF/LH was negatively correlated with letter identification score on the CORE Phonics Survey. This indicates that children with faster letter identification ability in the LH also had stronger letter ability as established by the standardized test.

hemispheric differences in orthographic knowledge. Because the RTs displayed by the children were long and likely less reliable, we restricted the analysis to accuracy as the dependent measure. An ANOVA with group (children, adults) and visual field (left, right) for word/letter matching revealed no main effect of group, $[F(1,28) = .067, p > .8]$ which indicates that we successfully titrated the overall level of difficulty across the groups. We did, however, obtain a significant interaction of group by visual field, $[F(1,28) = 5.8, p = .02]$, with higher accuracy for the RVF/LH than the LVF/RH in adults but not in children, as reported above. This interaction confirms the findings from the analyses performed for the two participant groups separately.

3.6. Relationship between left lateralization for letters and HSF visual information

The findings thus far are consistent with the account that there is no antecedent HSF bias that is integral to the LH that might serve as the trigger for the emergence of the left visual word processing superiority. In this final analysis, we took into account the fact that not all children performed equivalently on the divided-field letter matching task and that there was within-group variability in performance. In this final analysis, then, we examined individual differences in the relationship between spatial frequency and letter matching performance amongst the children. A Pearson correlation revealed a significant positive correlation between RT for letter matching in the RVF/LH and RT for HSF Gabor patches in the RVF/LH (see Fig. 8, $p = .018$). There was, however, also a significant correlation between RT for letter matching in the LVF/RH and RT for HSF Gabor patches in the LVF/RH perhaps suggesting that the previous correlation is non-specific (i.e., children who are faster may be faster across the board). To determine whether there was any specific association between the letter matching and HSF measures in the RVF/LH per se, we calculated difference scores across the two visual

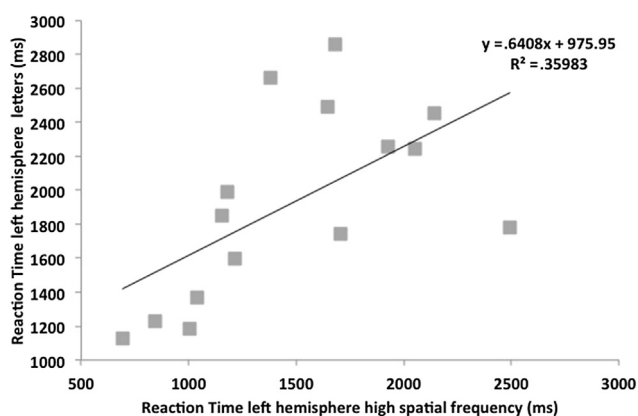


Fig. 8 – Children data. Reaction time for high spatial frequency Gabor patches in the RVF/LH was positively correlated with reaction time for processing letters appearing in the RVF/LH.

fields [RT for letters (RVF – LVF) and accuracy for HSF Gabor patches (RVF-LVF)] and computed the correlation between these measures. The result of this correlation was marginally significant, $p = .051$, suggesting that over and above possible general maturation and skill development in the children, there still remains an association between proficiency in letter discrimination and spatial frequency in the LH. Lastly, to determine whether it might be age rather than (or in addition to) letter recognition that is associated with the better LH HSF Gabor detection, we performed a stepwise regression analysis with RVF/LH HSF RT as the dependent variable and age as well as letter recognition accuracy and RT in the left and right visual fields as predictive variables (with $p < .05$ as threshold for model entry). The first variable entered was RT for letter recognition in the LVF/RH ($\beta = .8$, $t = 4.8$, $p < .000$; over and above that, accuracy for letter matching in the RVF/LH was entered ($\beta = -.35$, $t = 2.3$, $p < .05$). Age did not account for any variance over and above these two factors, indicating that it is letter recognition competence per se, rather than age, which is associated with HSF tuning of the LH.

Last, as a further test of the relation between reading acquisition and RVF processing in the children, we examined the correlation between performance on the CORE Phonics survey and performance on the high and low spatial frequency Gabor patch task in the two visual fields. There was a significant correlation between the composite CORE Phonics Survey score (see methods) and accuracy for HSF Gabor patch discrimination in the right ($p = .031$) but not left visual field ($p = .36$) and no correlation with accuracy for the low spatial frequency Gabor patch discrimination (both $p > .15$). This finding serves to demonstrate further that the emergence of reading skills is correlated with HSF tuning in the RVF/LH in the children.

Taken together, the results provide no evidence for the developmental emergence of HSF information that appears prior to the emergence of LH letter recognition skills. That one sees an association between the detection of HSF information in the RVF/LH and letter recognition skills in the RVF/LH (as well as with the Core Phonics measure) on an individual-by-individual basis suggests either that (i) the LH may become

tuned for HSF in tandem with the acquisition of orthographic skills or (ii) alternatively, although there is no clear way to establish causality, the relationship between HSF and orthography in the LH may be a consequence of letter knowledge acquisition in those children with more advanced orthographic competence (independent of age). If the latter were so, the exposure to print may induce the spatial frequency tuning of the LH rather than the other way round.

4. Discussion

The goal of this study was to examine the underlying basis for the LH lateralization of orthographic representations. Although both the RH and LH are activated in response to words, the LH is typically activated to a much greater extent (McCandliss, Cohen, & Dehaene, 2003; Wandell, Rauschecker, & Yeatman, 2012). At least two possible explanations have been posited for the LH specialization for word perception, one having to do with the need for closer communications with language-related areas in the LH (Behrmann & Plaut, 2013a, 2013b; Price & Devlin, 2011), and the other having to do with the bias or tuning of the LH for processing HSF information (Grabowska & Nowicka, 1996; Robertson & Ivry, 2000; Sergent, 1982). Of course, these accounts are not mutually exclusive, and both factors might contribute to word lateralization. In the current work, we determine whether a pre-existing bias for HSF visual information in the LH predisposes it to become specialized for word reading. This issue is of importance in understanding the mechanism that gives rise to the pattern of hemispheric organization observed in adulthood, more generally, as well as to a specific understanding of how the visual word form area emerges (to a greater degree) in the LH than RH.

To ascertain whether the LH HSF tuning (observed in adults) plays a causal role in the LH superiority for word processing, we used a divided-field task to index the hemispheric bias, as measured by RT, accuracy and IE, for HSF over LSF Gabor patches and for word stimuli in a group of 15 adults. Thereafter, we tested a group of 15 children (mean age 4.5 years) to characterize their letter recognition performance in the two visual fields, and to assess, as a group and at an individual level, whether an HSF bias in the LH pre-dates the emergence of the LH letter recognition superiority. If there is no preceding HSF bias in the LH, the HSF tuning observed in adult readers might potentially arise in concert with reading or be the effect of increased reading competence rather than its cause.

As expected, we found that adults displayed the typical RVF/LH over LVF/RH lateralization for word processing and the same superiority for detecting the presence of HSF over LSF Gabor patches. However, the same spatial frequency paradigm did not uncover a LH preference for HSF Gabor patches in the children, and no hemispheric asymmetries were observed. Similarly, using a slightly modified orthographic paradigm for the children, with letters rather than words, we found no LH advantage for letter discrimination, nor any other hemispheric asymmetries. This null effect was unlikely to be due to insufficient sensitivity of the measure as we found significant correlations between children's RTs to

letters in the RVF/LH and their level of letter identification ability as measured by the CORE Phonics Survey. Moreover, in a direct comparison between adults and children, there was a significant interaction with group in the word/letter performance, with only the adults showing a hemispheric advantage.

Interestingly, notwithstanding the absence of a hemispheric difference for either HSF or letter discrimination in children as a group, an analysis of the individual participant data did yield a significant correlation between RTs for HSF Gabor patches in the RVF/LH and RTs for letter stimuli in the RVF/LH in the young children. Although there was also a correlation with the RT for letter stimuli in the LVF/RH, this was weaker than for the RVF/LH (and thus a difference score between RTs in the two fields still yielded a correlation with HSF Gabor patch detection). Also, the HSF Gabor detection ability was correlated with performance on the Core Phonics survey, further affirming the association between spatial frequency and letter/reading competence in the LH. Thus, it appears that the degree to which a child has developed a RVF/LH advantage for letter stimuli is associated with the degree to which a child has developed a RVF/LH advantage for HSF information and, of note, this association is not contingent on age per se.

4.1. Directionality of spatial frequency processing and letter processing

One obvious conclusion from the results is that there is no a priori or essentialist LH/HSF tuning which then biases the LH to be optimized for word/letter processing. As evident in Fig. 8, there is a cluster of children who show relatively faster RTs for both letter discrimination and HSF detection in the RVF/LH. There is also a cluster of children who are slow on letter perception and HSF detection. Most relevant is the fact that there are no children in the upper left quadrant of the figure in which fast HSF detection is accompanied by slow letter discrimination. It is this particular pattern that would lead to the conclusion that HSF tuning in the LH determines or precedes the emergence of LH orthographic competence. This result argues against an innate visual-frequency processing bias that leads to the development of the visual reading area in the LH per se. Consistent with this is the finding that, in subjects with atypical right-hemisphere lateralization of the language network, the ventral visual reading area emerges in the right rather than in the LH (Cai et al., 2010).

We have argued, then, that there is no fundamental spatial frequency bias of the LH that triggers the acquisition of orthographic skills. Instead, the results are consistent with the idea that the lateralization of reading is tied to mechanisms associated with integrating visual perceptual processes with language representations (Price & Devlin, 2011), and that connectivity to language areas may even be the primary driving factor in establishing lateralization of visual word reading (Bouhali et al., 2014). A number of recent studies have suggested that it is not only top-down effects of language that serve as the possible driving force but that literacy even affects occipital areas much earlier than the visual word form area. For example, Szwed et al. (2011) showed that words, as

opposed to objects, are preferentially enhanced in retinotopic visual areas [see also (Dehaene et al., 2010; Szwed, Ventura, Querido, Cohen, & Dehaene, 2012)]. Finally, Rothlein and Rapp (2014) reported that letters are encoded in an occipital area much earlier than the VWFA. It remains possible that higher order language representations tune visual areas all the way down to retinotopic areas (or vice versa) and so causality and the pathway by which these effects occur once again remains to be determined.

Together, these findings argue against a causal role of HSF LH bias in the configuring of orthographic hemispheric asymmetry. We take this evidence as refuting a directional relationship between spatial frequency and word recognition LH superiority, and suggest, instead, that the development of LH visual and word representations and HSF bias in the LH may emerge in parallel. Alternatively, the HSF bias in the LH may be a result of orthographic tuning in the LH. In fact, in spite of the absence of any firm evidence, we favor this view – because it is unclear why HSF and orthography might emerge in parallel, it seems more parsimonious that the LH HSF might be a result of the orthographic tuning. We recognize, however, that compelling evidence for this view is elusive and that the use of a cross-sectional design may not suffice for this purpose.

4.2. Possible approaches to causality

One obvious methodological approach that could bear fruit in establishing a causal relationship between LH HSF and word processing is the adoption of a longitudinal design in which both spatial frequency and letter asymmetries are tracked together over time. Longitudinal studies are crucial because the acquisition of reading is one of the most complex cognitive feats that the brain achieves. As young children learn to recode print to sound, the brain undergoes intensive and highly specific experience-dependent learning, often on a daily basis. These learning experiences selectively train aspects of sensory processing and attention and learning to read changes the brain. Therefore, the identification of pre-reading biases is vital to understanding causation in reading acquisition and its hemispheric asymmetry (Goswami, 2014).

In fact, such a design has proven valuable in the past. Davidoff and Done (1984) conducted a longitudinal study of the visual field advantage for letter matching and concluded that the RVF/LH advantage for letters appeared readily as letter knowledge was achieved. This study found a subset of children who could not yet name letters and who did not display a RVF/LH advantage, and suggested that this advantage emerges only after letter knowledge is achieved. This study did not, however, measure spatial frequency analysis of these children and so this hemispheric bias and its role in word lateralization remains to be examined. In addition to the longitudinal measurement (and one that is somewhat easier to implement), a cross-sectional design could be applied such that a group of early reading children, ages (7–9) for example, are also tested, in order to investigate to what extent early reading abilities are associated with left lateralization for HSF and letters/words (see also Clark et al., 2014, for longitudinal neuroimaging study albeit on children with developmental dyslexia).

Having failed to establish a relationship between spatial frequency and word/letter recognition in the current study, we suggest that the superiority for orthographic processing in the LH is likely related to the fact that language is mediated by the LH in the majority of individuals. This view has been previously articulated by Dundas et al. (2013, 2014) who also go on to argue that the tuning of the LH to words arises due to pressure to maintain short connection length between visual and language areas. The VWFA appears to receive projections from visual cortex and has access to a pathway that can carry signals forward and backward to and from cortical language regions (Yeatman, Rauschecker, & Wandell, 2013). Indeed, the VWFA may have a privileged position in communicating information about word forms between visual and language areas (Devlin, Jamison, Gonnerman, & Matthews, 2006) and it is this close association, and the association with early, retinotopic cortical areas (Szwed et al., 2011), that triggers the LH lateralization of the VWFA and superior word recognition.

4.3. Spatial frequency and word reading

To our knowledge, no previous study has examined RVF/LH lateralization for high or low spatial frequency Gabor patches in young children. There are, however, many studies which point to the joint association of an HSF bias and visual word perception in the LH in adulthood, some of which pinpoint the same neural region as implicated in both domains (Roberts et al., 2012; Woodhead et al., 2011). But not all studies, even in adulthood, reveal a definitive association between these two domains. For example, a recent report of a patient with pure alexia demonstrates that, despite a significant reading deficit, this patient retained normal sensitivity to HSF gratings (Starrfelt, Nielsen, Habekost, & Andersen, 2013). This dissociation, however, may indicate that once the LH is tuned to HSF by reading, the reading system may no longer be directly reliant on HSF. It is also possible of course that the functional damage in this patient may impact aspects of reading that are distinct from those requiring HSF information (for example, integrating the letters into coherent word rather than the visual encoding of the letters per se).

4.4. Spatial frequency and the two hemispheres: a potential caveat

Considerable evidence supports the claim that the cerebral hemispheres in adults differ in their spatial frequency tuning, including differential sensitivity to particular frequency bands, with a good fit between LH tuning for those frequencies that are best suited for encoding written words. The nature of the spatial frequency tuning, however, is perhaps more complicated than this, with some studies showing no hemispheric specialization for particular frequency ranges (Di Lollo, 1981; Peterzell, 1991). For example, vertical gratings presented to the LVF and the RVF of participants evokes equivalent contrast-sensitivity functions and visible persistence durations in the two hemispheres (Peterzell, Harvey, & Hardyck, 1989). Similarly, when a pair of Gaussian windowed sinusoidal gratings were presented to the LVF and the RVF of both commissurotomy patients and healthy controls for same/different orientation judgment, there was no

indication of an interaction between visual field and spatial frequency of the gratings in this task (Fendrich & Gazzaniga, 1990). The absence of tuning for absolute spatial frequency bandwidth has led to alternative suggestion. One modification of the hemispheric-spatial frequency tuning is that it is not spatial frequency per se that is differentially processed by the two hemispheres but, rather, there is filtering by frequency (Double Filtering by Frequency; DFF). This view posits that, after attentional selection of a task-relevant frequency range, the LH amplifies high frequencies, whereas the RH amplifies low frequencies. The implication of this account in the context of the present paper is that, whereas we measured absolute frequency bands and the hemispheric response to these and to orthographic processing, it is the relative frequency that is the critical index. Whether there is a causal relationship between relative frequency (DFF) and the emergence of left lateralization for word processing, therefore, remains to be determined.

Additionally, we note that we have placed the majority of the emphasis in this paper on the LH but LH function may not be independent and may be contingent on variability of the RH (Dehaene et al., 2010; Seghier & Price, 2011). A final word of caution concerns the fact that letter recognition may be mediated by a different anatomical structure than word recognition (James, James, Jobard, Wong, & Gauthier, 2005), so it is possible that the adults and children in the present study are performing the orthographic task in different ways. Many of these cautionary comments require further investigation and clarification.

5. Conclusion

This study provides insight into the nature of hemispheric asymmetries, as well as their underlying origins. The current results offer no support for the claim that the LH is pre-tuned to HSF information (whether by hemispheric differences in receptive field size or by differences in the nature of the structural connectivity or through some other mechanism). The results support the theory that, during the pre-school years, roughly at the age of 4 and 5, before letter identification skills are strong, the hemispheres are not strongly organized based on spatial frequency. To the extent that one observes tuning for HSF information, this may emerge in tandem with orthographic skill acquisition or even be a consequence of reading experience. Either way, the critical result is that a LH HSF bias is unlikely to be a pre-existing cause of hemispheric lateralization of orthographic representations. In the future, it would be informative to probe this question further through a longitudinal study, tracking the development of left lateralization for HSF and for letters over the course of learning to read so as to elucidate possible mechanisms that underlie the hemispheric superiority for word recognition.

Acknowledgments

This research was supported by a grant from the National Science Foundation to MB (BCS-1354350) and by a Carnegie

Mellon Undergraduate Research Office Summer 2013 Undergraduate Research Fellowship (SURF) and Spring 2014 Small Undergraduate Research Grant (SURG). The authors thank Dr. Sharon Carver and the administrators/teachers of the Carnegie Mellon University Children's School for their support of this research. The authors thank Eva Dundas for her help and the use of her stimuli, Adrian Nestor for help with stimulus development, Noa Wolff-Fineout for her assistance with data analysis and David Plaut for helpful discussions.

REFERENCES

- Adams, R. J., & Courage, M. L. (2002). Using a single test to measure human contrast sensitivity from early childhood to maturity. *Vision Research*, 42(9), 1205–1210.
- Behrmann, M., & Plaut, D. C. (2013a). Bilateral hemispheric processing of words and faces: evidence from word impairments in Prosopagnosia and face impairments in pure alexia. *Cerebral Cortex*, 24(2), 1102–1118.
- Behrmann, M., & Plaut, D. C. (2013b). Distributed circuits, not circumscribed centers, mediate visual recognition. *Trends in Cognitive Sciences*, 17(5), 210–219.
- Behrmann, M., Plaut, D. C., & Nelson, J. (1998). A literature review and new data supporting an interactive account of letter-by-letter reading. *Cognitive Neuropsychology*, 15, 7–51.
- Bouhali, F., Thiebaut de Schotten, M., Pinel, P., Poupon, C., Mangin, J. F., Dehaene, S., et al. (2014). Anatomical connections of the visual word form area. *Journal of Neuroscience*, 34(46), 15402–15414.
- Cai, Q., Paulignan, Y., Brysbaert, M., Ibarrola, D., & Nazir, T. A. (2010). The left ventral occipito-temporal response to words depends on language lateralization but not on visual familiarity. *Cerebral Cortex*, 20(5), 1153–1163.
- Clark, K. A., Helland, T., Specht, K., Narr, K. L., Manis, F. R., Toga, A. W., et al. (2014). Neuroanatomical precursors of dyslexia identified from pre-reading through to age 11. *Brain*, 137(Pt 12), 3136–3141.
- Davidoff, J. B., & Done, D. J. (1984). A longitudinal study of the development of visual field advantage for letter matching. *Neuropsychologia*, 22(3), 311–318.
- Dehaene, S., Pegado, F., Braga, L. W., Ventura, P., Nunes Filho, G., Jobert, A., et al. (2010). How learning to read changes the cortical networks for vision and language. *Science*, 330(6009), 1359–1364.
- Devlin, J. T., Jamison, H. L., Gonnerman, L. M., & Matthews, P. M. (2006). The role of the posterior fusiform gyrus in reading. *Journal of Cognitive Neuroscience*, 18(6), 911–922.
- Di Lollo, V. (1981). Hemispheric symmetry in duration of visible persistence. *Perception & Psychophysics*, 29(1), 21–25.
- Diamond, L., & Thorsen, B. J. (2008). *Assessing reading: Multiple measures* (2nd ed.). Arena Press.
- Dundas, E. M., Plaut, D. C., & Behrmann, M. (2013). The joint development of hemispheric lateralization for words and faces. *Journal of Experimental Psychology: General*, 142(2), 348–358.
- Dundas, E. M., Plaut, D. C., & Behrmann, M. (2014). An ERP investigation of the co-development of hemispheric lateralization of face and word recognition. *Neuropsychologia*, 61C, 315–323.
- Fendrich, R., & Gazzaniga, M. (1990). Hemispheric processing of spatial frequencies in two commissurotomy patients. *Neuropsychologia*, 28(7), 657–663.
- Fintzi, A. R., & Mahon, B. Z. (2014). A bimodal tuning curve for spatial frequency across left and right human orbital frontal cortex during object recognition. *Cerebral Cortex*, 24(5), 1311–1318.
- Goswami, U. (2014). The neural basis of dyslexia may originate in primary auditory cortex. *Brain*, 137(Pt 12), 3100–3102.
- Grabowska, A., & Nowicka, A. (1996). Visual-spatial-frequency model of cerebral asymmetry: a critical survey of behavioral and electrophysiological studies. *Psychological Bulletin*, 120(3), 434–449.
- Hsiao, J. H., Cipollini, B., & Cottrell, G. W. (2013). Hemispheric asymmetry in perception: a differential encoding account. *Journal of Cognitive Neuroscience*, 25(7), 998–1007.
- Hsiao, J. H., & Cottrell, G. W. (2009). Not all visual expertise is holistic, but it may be leftist: the case of Chinese character recognition. *Psychological Science*, 20(4), 455–463.
- Hsiao, J. H., & Lam, S. M. (2013). The modulation of visual and task characteristics of a writing system on hemispheric lateralization in visual word recognition—a computational exploration. *Cognitive Science*, 37(5), 861–890.
- Hsiao, J. H., Shieh, D. X., & Cottrell, G. W. (2008). Convergence of the visual field split: hemispheric modeling of face and object recognition. *Journal of Cognitive Neuroscience*, 20(12), 2298–2307.
- Ivry, R., & Robertson, L. C. (1998). *The two sides of perception*. Cambridge, MA: MIT Press.
- Jablonowska, K., & Budhoska, W. (1976). Hemispheric differences in the visual analysis of the verbal and non-verbal material in children. *Acta Neurobiologiae Experimentalis*, 36, 693–701.
- James, K. H., James, T. W., Jobard, G., Wong, A. C. N., & Gauthier, I. (2005). Letter processing in the visual system: different activation patterns for single letters and strings. *Cognitive Affective Behavioral Neuroscience*, 5(4), 452–466.
- Kitterle, F. L., Christman, S., & Hellige, J. B. (1990). Hemispheric differences are found in the identification, but not the detection, of low versus high spatial frequencies. *Perception & Psychophysics*, 48(4), 297–306.
- Majaj, N. J., Pelli, D. G., Kurshan, P., & Palomares, M. (2002). The role of spatial frequency channels in letter identification. *Vision Research*, 42(9), 1165–1184.
- Maurer, U., Brem, S., Bucher, K., & Brandeis, D. (2005). Emerging neurophysiological specialization for letter strings. *Journal of Cognitive Neuroscience*, 17(10), 1532–1552.
- McCandliss, B. D., Cohen, L., & Dehaene, S. (2003). The visual word form area: expertise for reading in the fusiform gyrus. *Trends in Cognitive Sciences*, 7(7), 293–299.
- Mercure, E., Dick, F., Halit, H., Kaufman, J., & Johnson, M. H. (2008). Differential lateralization for words and faces: category or psychophysics? *Journal of Cognitive Neuroscience*, 20(11), 2070–2087.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, 9(1), 97–113.
- Peterzell, D. H. (1991). On the nonrelationship between spatial frequency and cerebral hemispheric competence. *Brain and Cognition*, 15, 62–68.
- Peterzell, D. H., Harvey, L. O., Jr., & Hardyck, C. D. (1989). Spatial frequencies and the cerebral hemispheres: contrast sensitivity, visible persistence, and letter classification. *Perception & Psychophysics*, 46(5), 443–455.
- Peyrin, C., Chauvin, A., Chokron, S., & Marendaz, C. (2003). Hemispheric specialization for spatial frequency processing in the analysis of natural scenes. *Brain and Cognition*, 53(2), 278–282.
- Price, C. J., & Devlin, J. T. (2011). The interactive account of ventral occipitotemporal contributions to reading. *Trends in Cognitive Sciences*, 15(6), 246–253.
- Proverbio, A. M., Zani, A., & Avella, C. (2002). Hemispheric asymmetries for spatial frequency discrimination in a selective attention task. *Brain and Cognition*, 34, 311–320.
- Roberts, D. J., Woollams, A. M., Kim, E., Beeson, P. M., Rapcsak, S. Z., & Lambon Ralph, M. A. (2012). Efficient visual object and word recognition relies on high spatial frequency coding in the left posterior fusiform gyrus: evidence from a

- case-series of patients with ventral occipito-temporal cortex damage. *Cerebral Cortex*. <http://dx.doi.org/10.1093/cercor/bhs224>.
- Robertson, L. C., & Ivry, R. (2000). Hemispheric asymmetries: attention to visual and auditory primitives. *Current Directions in Psychological Science*, 9(2), 59–64.
- Rossion, B., Joyce, C. A., Cottrell, G. W., & Tarr, M. J. (2003). Early lateralization and orientation tuning for face, word, and object processing in the visual cortex. *NeuroImage*, 20(3), 1609–1624.
- Rothlein, D., & Rapp, B. (2014). The similarity structure of distributed neural responses reveals the multiple representations of letters. *NeuroImage*, 89, 331–344.
- Schlaggar, B. L., Brown, T. T., Lugar, H. M., Visscher, K. M., Miezin, F. M., & Petersen, S. E. (2002). Functional neuroanatomical differences between adults and school-age children in the processing of single words. *Science*, 296(5572), 1476–1479.
- Schlaggar, B. L., & McCandliss, B. D. (2007). Development of neural systems for reading. *Annual Review of Neuroscience*, 30, 475–503.
- Schneider, W., Eschman, A., & Zuccolotto, A. (2002). *E-prime user's guide*. Pittsburgh, PA: Psychology Software Tools.
- Seghier, M. L., & Price, C. J. (2011). Explaining left lateralization for words in the ventral occipitotemporal cortex. *Journal of Neuroscience*, 31(41), 14745–14753.
- Sergent, J. (1982). The cerebral balance of power: confrontation or cooperation. *Journal of Experimental Psychology: Human Perception Vision Research and Performance*, 8, 253–273.
- Sergent, J., & Hellige, J. B. (1986). Role of input factors in visual-field asymmetries. *Brain and Cognition*, 5, 174–179.
- Starrfelt, Nielsen, Habekost, & Andersen. (2013). How low can you go? Spatial frequency sensitivity in a patient with pure alexia. *Brain & Language*, 126, 188–192. <http://dx.doi.org/10.1016/j.bandl.2013.05.006>.
- Szwed, M., Dehaene, S., Kleinschmidt, A., Eger, E., Valabregue, R., Amadon, A., et al. (2011). Specialization for written words over objects in the visual cortex. *NeuroImage*, 56(1), 330–344.
- Szwed, M., Ventura, P., Querido, L., Cohen, L., & Dehaene, S. (2012). Reading acquisition enhances an early visual process of contour integration. *Developmental Science*, 15(1), 139–149.
- Tadros, K., Dupuis-Roy, N., Fiset, D., Arguin, M., & Gosselin, F. (2013). Reading laterally: the cerebral hemispheric use of spatial frequencies in visual word recognition. *Journal of Vision*, 13(1), 4.
- Townsend, J., & Ashby, F. (1983). *The stochastic modelling of elementary psychological processes*. Cambridge: Cambridge University Press.
- Turkeltaub, P. E., Gareau, L., Flowers, D. L., Zeffiro, T. A., & Eden, G. F. (2003). Development of neural mechanisms for reading. *Nature Neuroscience*, 6(7), 767–773.
- Wandell, B. A., Rauschecker, A. M., & Yeatman, J. D. (2012). Learning to see words. *Annual Review of Psychology*, 63, 31–53.
- Woodhead, Z. V., Wise, R. J., Sereno, M., & Leech, R. (2011). Dissociation of sensitivity to spatial frequency in word and face preferential areas of the fusiform gyrus. *Cerebral Cortex*, 21(10), 2307–2312.
- Yeatman, J. D., Rauschecker, A. M., & Wandell, B. A. (2013). Anatomy of the visual word form area: adjacent cortical circuits and long-range white matter connections. *Brain and Language*, 125, 146–155.