Research report

The relationship between visual word and face processing lateralization in the fusiform gyri: A cross-sectional study

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A B S T R A C T

Visual words and faces activate similar networks but with complementary hemispheric asymmetries, faces being lateralized to the right and words to the left. A recent theory proposes that this reflects developmental competition between visual word and face processing. We investigated whether this results in an inverse correlation between the degree of lateralization of visual word and face activation in the fusiform gyr. 26 literate right-handed healthy adults underwent functional MRI with face and word localizers. We derived lateralization indices for cluster size and peak responses for word and face activity in left and right fusiform gyri, and correlated these across subjects. A secondary analysis examined all face- and word-selective voxels in the inferior occipitotemporal cortex. No negative correlations were found. There were positive correlations for the peak MR response between word and face activity within the left hemisphere, and between word activity in the left visual word form area and face activity in the right fusiform face area. The face lateralization index was positively rather than negatively correlated with the word index. In summary, we do not find a complementary relationship between visual word and face lateralization across subjects. The significance of the positive correlations is unclear: some may reflect the influences of general factors such as attention, but others may point to other factors that influence lateralization of function.

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1. Introduction

Face and visual word recognition are both examples of expert visual processing, requiring fine discriminations between highly similar stimuli. Neuroimaging studies show that the processing of visual words and faces involves networks that include regions in inferior temporal cortex that respond more to faces or visual words than to any other categories of objects. The ‘fusiform face area’ (FFA) in the mid portion of the fusiform gyrus (Kanwisher et al., 1997a, 1997b), is thought to be involved in the processing of unique facial identity (Haxby et al., 2000a, 2000b), while the ‘visual word form area’ (VWFA) is another mid-fusiform region that shows a selectivity for visually presented words (Cohen et al., 2000).

A consistent observation about these networks and regions is that they show a lateralized asymmetry. The FFA is more often identified and larger in both size and magnitude of response in the right than in the left hemisphere (Davies-Thompson and Andrews, 2012; Rossion et al., 2012), while the VWFA (Cohen et al., 2000) is often more identified in the left than the right hemisphere (Cohen et al., 2000, 2002a, 2002b; Dehaene and Cohen, 2011; Szved et al., 2011). These anatomic asymmetries have functional parallels. Tachistoscopic studies show a right visual field bias for words and a left field bias for faces (Leehey and Cahn, 1979; Levine and Banich, 1982; Levine and Koch-Weser, 1982), and the latter has been correlated with the degree of face activation in the right hemisphere on functional MRI (Yovel et al., 2008). Studies using evoked-potentials consistently show greater N170 potentials for words in the left occipital cortex (Maurer et al., 2008; Mercure et al., 2011) and for faces in the right occipital cortex (Scott, 2006). Neuropsychologically, the impaired face recognition of prosopagnosia typically follows damage to bilateral or right occipito-temporal cortex (de Renzi, 1986; Haxby et al., 2000a, 2000b; Sergent and Vildernure, 1989), while the impaired reading of alexia is associated with left occipito-temporal damage (Kawahata et al., 1988; Sakurai et al., 1994).

Besides their complementary lateralization, there are additional relevant observations about the neural bases of face and
word processing. For one, both faces and words activate similar bilateral networks, involving fusiform, lateral temporal and inferior frontal regions, among others (Barton et al., 2010a, 2010b; Haxby et al., 2000a, 2000b). For another, given that the lateralization of face and word regions is only partial, there remains significant overlap in each hemisphere between the regions activated by faces and those activated by words (Nestor et al., 2013). These points have led to recent speculations that the lateralized hemispheric specialization for words and faces evolves through competition between face and word processing for the neural resources in these object-recognition networks (Behrmann and Plaut, 2013; Dundas et al., 2013). Thus, while the recycling hypothesis initially proposed that the acquisition of literacy is accompanied by co-opting of object-recognition resources by word processing (Dehaene et al., 2010), recent accounts suggest that this specifically targets neural substrates that might otherwise be devoted to face processing (Plaut and Behrmann, 2011). Efficiency constraints to maximize local over long-range connections may exert pressure to lateralize visual word processing to the left hemisphere, where non-visual language processing is situated. In this view, the right lateralization of face processing may follow as a consequence of the left lateralization of word processing.

Other work has disputed the competition hypothesis. First, there are observations that a right hemisphere preference to faces is already present in newborns (de Heering and Rossion, 2015) and in monkeys (Zangenehpour and Chaudhuri, 2005), and that visual input to the right hemisphere during infancy is necessary for face expertise to develop (Le Grand et al., 2003). These suggest that a right hemisphere bias for faces may be innate.

Nevertheless, the presence of an innate right hemisphere bias and the competition hypothesis are not necessarily mutually exclusive phenomena. A competition for resources between words and faces would predict that the left dominance of word processing and the right dominance of face processing have a non-arbitrary relationship in human subjects. If the neural resources of the left and right hemispheres for which faces and words compete are finite, then one possible outcome would be that the degree of lateralization of one would be inversely correlated with that of the other across a sample of the population. That is, given that the degree of lateralization for words and faces varies across subjects, one might expect that a competition that resulted in more left and fewer right hemispheric resources being devoted to visual words would also create a strongly lateralized face processing system, with more right and less left hemispheric activation by faces. On the other hand, a subject with more balanced visual word activation across left and right fusiform regions would also be expected to have a less asymmetric face processing system.

Some suggestive evidence for this predicted relationship between word and face activation has been produced. A study reported that the magnitude of the N170 potential for faces in the right hemisphere were positively correlated with those for words in the left hemisphere (Dundas et al., 2014). However, another study using functional MRI did not find a correlation between the lateralization of the FFA and VWFA (Pinel et al., 2015). Hence the issue is not yet settled. To test this prediction further, we examined a cohort of right-handed literate subjects with functional neuroimaging. We used standard localizers of face and word activation to determine if there was an inverse correlation across the cohort between the left/right balance of visual word activity and that for face activity.

2. Results

2.1. Same-ROI analysis

There was a positive correlation between the MR responses of the peak voxels activated for faces and those for words in both the left FFA ($r=0.68, p<0.001$) and left VWFA ($r=0.55, p<0.005$). Thus subjects with a greater response to faces had a greater response to words in these regions (Fig. 1A). Face and word MR responses were not correlated in the right FFA ($r=0.17, p=0.42$) but there was a trend to a positive correlation in the right VWFA ($r=0.36, p=0.09$).

When we examined the lateralization index (Fig. 1B), there was a positive correlation between the degree of lateralization of face activity and that for words within FFA regions ($r=0.49, p<0.05$), but not within VWFA regions ($r=0.02, p=0.93$). Including subjects’ handedness scores, cortical thickness, and cortical volume as additional regressors did not significantly change the model ($P's > 0.24$) and showed again a positive correlation for the lateralization indices within the FFA ($r=0.45, p<0.05$) but not in the VWFA ($r=0.02, p=0.93$).

2.2. Different-ROIs analysis

This analysis examined the relationship between regions in their response to their preferred stimulus (i.e. the response to faces in FFA regions versus the response to words in VWFA regions). For the numbers of voxels activated by the localizers, there was no correlation between the activation by words in VWFA regions and the activation by faces in the FFA regions, in either the left hemisphere ($r=-0.14, p=0.49$) or right hemisphere ($r=-0.09, p=0.65$). For the peak MR response, there was a positive correlation in the left hemisphere between the scores for faces in FFA regions and those for words in VWFA regions ($r=0.55, p<0.005$), but not in the right hemisphere ($r=0.32, p=0.11$) (Fig. 2A).

The lateralization indices for the numbers of voxels did not show any correlation between face activation in FFA regions and word activation in VWFA regions. Including handedness and cortical volume thickness did not change the model ($P's > 0.52$), but including cortical thickness did, though the correlation was still not significant ($r=0.20, p=0.37$). For the peak MR responses, however, there was a positive correlation between the lateralization index for word activation in the VWFA regions and face activation in the FFA regions ($r=0.41, p<0.05$) (Fig. 2B). Including subjects’ handedness scores, cortical thickness, and cortical volume as additional regressors did not significantly change the model ($P's > 0.27$) and a similar positive correlation was still found ($r=0.47, p<0.05$). However, this was driven by a single data-point (in the lower-left corner of Fig. 2B); repeating the correlation without this data-point resulted in a non-significant correlation ($r=0.27, p=0.21$).

Finally, we performed an additional correlational analysis, to investigate parallels with a prior report that the magnitude of the N170 potential for faces in the right hemisphere were positively correlated with those for words in the left hemisphere (Dundas et al., 2014). Thus we studied the relationship between the response to words in the left VWFA and the responses to faces in the right FFA. This showed no correlation for the number of voxels ($r=0.01, p=0.93$), but a positive correlation for the peak MR response ($r=0.44, p<0.022$). The positive correlation was even stronger when fusiform cortical thickness ($r=0.57, p<0.003$) and cortical volume ($r=0.54, p<0.006$) were taken into account.

At first glance, these last results might be taken as supporting the hypothesis that stronger lateralization for words is associated with stronger lateralization for faces. However, greater activation for faces in one hemisphere cannot be taken as indicating a more
Fig. 1. Correlations in ‘same regions-of-interest’ analysis. (A) The peak responses to words and faces within each region of interest. Graphs of the left are from the FFA regions, and graphs on the right from the VWFA regions. Top graphs are from the left hemisphere and middle graphs are from the right hemisphere. Lines indicate linear regression, with correlation coefficients (r) and significant shown, with bold lines and numbers indicating significant correlations. Units on the y-axis are z-scores (for faces > scrambled faces or words > scrambled words). (B) The lateralization indexes for these peak responses. Positive values indicate greater activation in the left hemisphere. Left graph is for activity identified within the boundaries of the FFA regions, and right graph is for activity within the VWFA regions. Full correlations are shown in black ink; numbers in grey indicate correlations after controlling for handedness, cortical thickness, and cortical volume. Bold lines and numbers indicate significant correlations.
asymmetric lateralization of faces. To support that inference one also needs to know how activation for faces in one hemisphere is related to activation for faces in the other, and likewise for words. The inference would be supported if there were either a negative or no correlation. However, for faces we find instead a positive correlation between the peak MR responses in the right FFA and those in the left FFA ($r = 0.65$, $p < 0.0003$) and a trend for words between the right and left VWFA ($r = 0.37$, $p = 0.06$). Again, these positive correlations are stronger when we take into account cortical thickness (faces, right versus left FFA: $r = 0.59$, $p < 0.002$; words, right versus left VWFA: $r = 0.49$, $p < 0.013$) or cortical volume (faces, right versus left FFA: $r = 0.54$, $p < 0.002$; words, right versus left VWFA: $r = 0.42$, $p < 0.036$). Thus, the positive correlations we find between words and faces both within and between the hemispheres in our ‘between ROI’ analysis reflect the fact that subjects with greater activation for faces also had greater activation for words, but do not point to an inverse relationship between the lateralization of faces and words.

2.3. Inferior temporal analysis

For the total number of voxels activated in inferotemporal cortex, there was no correlation between face and word activation in either the left ($r = -0.27$, $p = 0.90$) or right hemisphere ($r = 0.08$, $p = 0.73$) (Fig. 3A). For the average of the peak MR responses from all activated clusters, there was a trend to a positive correlation between face and word activity in the left ($r = 0.34$, $p = 0.08$) but not the right hemisphere ($r = -0.00$, $p = 0.99$).

The lateralization indices (Fig. 3B) also showed no correlation between words and faces for either the total number of voxels responding ($r = -0.13$, $p = 0.59$) or the averaged peak responses ($r = 0.08$, $p = 0.73$). Including subject’s handedness scores, cortical volume, and cortical thickness as additional variables did not improve the model ($P’s > 0.38$), and led to similar insignificant correlations for the number of voxel analysis ($r = -0.10$, $p = 0.66$) and the peak MR response analysis ($r = -0.03$, $p = 0.91$).
Fig. 3. Correlations in inferior temporal analysis (all voxels). (A) number of voxels activated (left graphs) and average of the peak responses of all clusters (right graphs). Top graphs are for the left and middle graphs for the right hemisphere. Lines indicate linear regression, with correlation coefficients ($r$) and significance shown, with bold lines and numbers indicating significant correlations. Units are z-scores (faces > scrambled faces or words > scrambled words). (B) The lateralization indexes for number of voxels (left graph) and peak responses (right graph), in which positive values indicate greater activation in the left hemisphere. Full correlations are shown in black ink; numbers in grey indicate correlations after controlling for handedness, cortical thickness, and cortical volume. Bold lines and numbers indicate significant correlations (none were found).
3. Discussion

We hypothesised that, if there is competition between face and word processing for neural resources in inferior temporal cortex (Dundas et al., 2013; Plaut and Behrmann, 2011), we would find that in any given region of a hemisphere, greater activation for one of these two stimuli would be associated with less activation for the other, resulting in a negative correlation across subjects. Instead, we found positive correlations for peak MR responses within left-sided regions of interest, between the left FFA and left VWFA, and between the maximally active voxels in left and right inferotemporal cortex, but no other correlations in the right hemisphere or for the number of voxels activated. Second, we also hypothesised that the magnitude of hemispheric asymmetry as represented in a lateralization index would show a complementary relationship between visual word and face activation, and hence a negative correlation between face and word indices. Instead, we again found a positive correlation for the lateralization indices of peak MR responses both within the FFA regions and between the FFA and VWFA regions. Otherwise, there was little evidence in other dependent variables or analyses for any correlation, and this did not change whether or not outliers were included or whether the analysis was adjusted for handedness, cortical thickness and volume.

The positive correlations found within a region or hemisphere, particularly on the left side, may suggest that the ability or need to recruit resources to process words is correlated in some fashion with the ability or need to do the same for face processing. However, this finding needs to be interpreted with caution. Non-specific factors such as attention can modulate the degree of activation in visual processing areas (Bressler et al., 2013; Schwartz et al., 2005) and a positive correlation of word and face activation across subjects may simply be due to variations in attention across subjects. The positive correlation found for the lateralization indices may also be a more specific effect, since it is not clear that a general modulation of signals by attention or other factors would alter the degree of hemispheric asymmetry. Nevertheless, one cannot definitively exclude a priori the possibility that general factors could enhance the activation in a dominant hemisphere differently than that in the non-dominant one.

We analyzed both the peak MR responses and the number of voxels activated in a region. At this point it is not clear which is a better index of the amount of neural resources recruited by a task. We did not find any correlations when using the cluster size (i.e. number of voxels) as the response measure. Unlike the case of peak MR responses, which have the advantage of being unaffected by the statistical threshold used to define activation, cluster sizes are heavily dependent upon the choice of threshold, and one can question whether our use of a variable threshold to set the side of least activation at 10 voxels may have introduced distortions into the lateralization index we calculated. However, this method was necessary to identify a minimum degree of activation in the minor hemispheres (left for faces and right for words) to enter into the lateralization index. Failure to do so would have resulted in a lateralization index of 1.00 for a number of subjects, a ceiling effect that would not accurately capture the magnitude of asymmetry of their activation. In any case, no significant correlations were observed in the analysis of number of voxels activated in the inferior temporal cortex, which used a fixed threshold.

The absence of a negative correlation in our study does not mean that competition between resources for face and word processing in the occipito-temporal cortex does not exist. It is important to consider a number of technical points. For one, all our subjects were right-handed. Previous studies show that handedness can influence the degree of lateralization of word (Cai et al., 2007) and face processing (Bukowski et al., 2013; Willems et al., 2010). For example, a left-sided lateralization of face areas was found in 17% of right-handed but 28% of left-handed subjects (Bukowski et al., 2013; Rossion et al., 2012). It may be that broadening the handedness spectrum of subjects would generate a wider range of lateralization indices, and different correlations may then emerge.

Second, our study is a cross-sectional survey of literate adults. This is a similar strategy to that used in one prior study that, in distinction to our results, found a negative correlation between the response to visual words and that to faces in the left fusiform gyrus for literate but not illiterate adults (Dehaene et al., 2010). However, this latter study did not examine the effects in the right hemisphere or a lateralization index, so one cannot make definitive inferences from this result regarding the emergence of hemispheric asymmetries in word and face processing. A longitudinal study of the lateralization of word and face activity in children or adults during the acquisition of literacy would be the best way of demonstrating the effects of competition during development. Short of that, recent cross-sectional studies of different age cohorts have found that children possess only a right hemifield superiority for words but not the left hemifield superiority for faces that is seen in adults (Dundas et al., 2013). Similarly an event-related potential study also reported that children showed a larger N170 potential for words on the left hemisphere but no hemispheric asymmetry in the N170 potential for faces, with the latter being found only in adults (Dundas et al., 2014).

Finally, a review of face imaging studies (Dien, 2009) noted that the use of different subtractive baseline conditions in localizer protocols may produce different patterns of face lateralization. The use of non-face visual objects resulted in greater right-lateralization (Gauthier et al., 1999; Haxby et al., 1999; Rhodes et al., 2004), while less lateralization was observed in studies that used just fixation or scrambled faces (Gilaie-Dotan and Malach, 2007; Ishai et al., 2002; Puce et al., 1995). A wide range of subtractive conditions have also been used for visual word processing studies – for review, see (Barton et al., 2010a, 2010b); how these affect the apparent lateralization of word processing has not yet been evaluated in a similar manner. However, we found that the results were very similar for the response in the FFA to words and faces when using a conjunction contrast (i.e. (faces > objects)/(faces > scrambled faces)) as when comparing the response to scrambled stimuli only. Regardless, the report of (Dien, 2009) indicates that the simple technical issue of the baseline subtractive condition may have consequences for the search for a complementary relationship between the lateralization of word and face processing using fMRI. Replication of our study with different baseline conditions would be an important next step.

One previous study (Dundas et al., 2014) reported a correlation between the magnitude of the N170 for words in the left hemisphere and that for faces in the right hemisphere. In an analogous fashion, we too found a correlation between the peak MR responses for words in the left VWFA and that for faces in the right FFA. However, as we discussed in the results above, such results do not prove the existence of an inverse relationship in the lateralization of activity for words and faces. Rather, we find positive correlations 1) between peak MR responses for words and faces within each hemisphere, 2) between faces in the left and faces in the right hemisphere, and 3) between words in the left and words in the right hemisphere. All this simply means that a) for a given stimulus, greater activation in one hemisphere is associated with greater activation in the other, and b) that greater activation for faces is associated with greater activation for words. This underlines the importance of a lateralization index to capture the degree of hemispheric asymmetry of activation.

As discussed above, there may be non-specific reasons why activation for words and faces may show a positive correlation
across subjects. However, it is more difficult to attribute a positive correlation between the lateralization indices for words and faces to general factors such as attention. One possible reason for a positive correlation is that there are external factors that influence the lateralization of both words and faces. Indeed, any inverse relationship between word and face lateralization may be obscured if the external influences are the dominant factor driving lateralization. We considered the possibility of handedness (Bukowski et al., 2013; Cai et al., 2007; Willems et al., 2010) and hemispheric asymmetries in structural neural resources as indexed by the cortical thickness and volume of the fusiform gyri; however, accounting for these still did not yield an inverse relationship between word and face lateralization. Nevertheless, other factors remain to be explored. Language dominance may have an important influence on the lateralization of other processes, as well as competition for visual processing resources by other objects besides faces and words, particularly those for which the subject has acquired expertise (Behrmann et al., 2005).

Along these lines are the findings of another study of the lateralization of the response to words and faces in the VWFA and FFA (Pinel et al., 2014). Like us they also failed to find an inverse correlation between words and faces; however, they did not observe positive correlations either. (One possible reason is the difference between their study and ours in localising regions of interest: while we identified regions on an individual subject level, which can take into account individual anatomic variations, they localized regions from activity observed at the group level.) Perhaps more interestingly, they observed an inverse correlation between the response to faces in the FFA and the response to spoken language in the STS. This is consistent with our inference from the positive correlations between visual word and face activity that other factors such as language may play a role in the hemispheric asymmetries that develop for both words and faces.

In summary, we did not find an inverse relationship between the lateralization of word and face activation using functional neuroimaging in this cross-sectional study of healthy subjects. Rather, there were positive correlations between lateralization indices for VWFA and FFA regions: the more right-hemisphere biased a subject’s face activation was, the more right-hemisphere biased their word activation was also. These results do not support a competition between face and visual word processing as a contributing factor to the complementary lateralization of these processes; they do not disprove it – more dominant influences that also drive hemispheric asymmetry may mask an inverse relationship between words and faces. Further work to identify these factors and to study the evolution of word and face lateralization during development would be important next steps.

4. Methods

4.1. Subjects

Twenty-six healthy participants with no history of neurological dysfunction, vascular disease or cognitive complaints took part in the study (16 females, mean age = 26, range 21–36). All participants were right-handed with corrected visual acuity of 20/20. A handedness score was obtained for each subject using the Edinburgh handedness questionnaire (Oldfield, 1971). The protocol was approved by the institutional review boards of the University of British Columbia and Vancouver General Hospital, and written informed consent was obtained for all subjects in accordance with The Code of Ethics of the World Medical Association, Declaration of Helsinki.

4.2. Imaging parameters

Subjects were scanned in a Philips 3.0 T scanner at the UBC MRI Research Centre. T2*-weighted scans using echo planar imaging were used to collect data from 36 interleaved axial slices (TR 2000 ms, TE 30 ms, FOV = 240 × 216 mm, 3 mm thickness with 1 mm gap, voxel size 3 × 3 mm, 128 mm reconstruction matrix, reconstructed voxel size 1.88 × 1.6 mm). These were co-registered onto a T1-weighted anatomical image (EPI) sequence, 170 axial slices, FOV = 256 × 200 mm, voxel size = 1 × 1 mm, slice thickness 1 mm, from each participant.

4.3. Localizer scans

Localizer scans were used to identify regions of visual cortex responding to English words and faces (Fig. 4). The HVEM dynamic face multiple localizer scan (Fox et al., 2009) was run twice on each subject to identify face-selective regions of the visual cortex. The localizer consisted of grayscale video clips of faces, bodies, objects, Fourier-phase scrambled faces, and Fourier-phase scrambled objects. Each stimulus block included 6 video clips lasting
1.5 s separated by a 500 ms blank screen, resulting in 12 s stimulus blocks. Stimulus blocks were separated by a 12 s fixation cross. Each condition was repeated 5 times per run.

A scan to localise word-selective regions of the visual cortex was also run twice on each subject (Barton et al., 2010a, 2010b). The localizer consisted of grayscale images of 3- or 4-letter English words, Korean words, and Fourier-phase scrambled English words. Each stimulus block included 15 images lasting 500 ms separated by a 300 ms blank screen, resulting in 12 s stimulus blocks. Stimulus blocks were separated by a 12 s fixation cross. Each condition was repeated 5 times per run.

In all functional scans, attention was monitored by asking participants to press a button on an MRI-compatible button-box when the same video clip or image was presented twice in a row.

4.4. fMRI analysis

Statistical analysis of the fMRI data was carried out using FEAT (http://www.fmrib.ox.ac.uk/fsl; (Smith et al., 2004)). The initial 8 s of data from each scan were removed to minimize the effects of magnetic saturation. Motion correction was followed by spatial smoothing (Gaussian, FWHM 6 mm) and temporal high-pass filtering (cut-off of 0.01 Hz).

Ideally, a conjunction contrast (i.e. (faces = objects)∩(faces > scrambled faces)) would be used to isolate face- and word-selective regions of interest. However, while a conjunction contrast for faces enabled us to identify the bilateral FFA in all 26 subjects, the complementary contrast for words ((English words = Korean words)∩(English words > scrambled words)) allowed us to identify the left VWFA in 19 subjects but the right VWFA in only 6 subjects. This is in line with a previous study in which we found that the VWFA responded equally to several forms of visual symbols, including English words and Korean words (Muayqil et al., 2015). As lateralization indices require subjects to have bilateral responses, using this conjunction contrast only allowed us to examine the response from 6 subjects, and we were therefore unable to conduct analysis for either 1) the response to faces and words within the VWFA, nor 2) the more crucial comparison between the FFA and VWFA. We were however, able to examine the response to faces and words within the FFA, where we found no significant positive or negative correlations (Supplementary Fig. 1). In order to circumvent this issue, word-selective regions were determined by the contrast English words > scrambled English words (P < 0.001, uncorrected), which enabled us to identify the right and left VWFA in the majority of subjects. For symmetry, we therefore used the corresponding contrast (faces > scrambled faces) to identify the face-selective regions.

### Table 1

Peak MNI coordinates of the region of interest analysis and most significant voxels in the inferior temporal cortex. Also shown are the average peak MR response for all clusters, along with the average total area showing significant activity (P < 0.001), in the inferior temporal cortex analysis. For comparison across studies, cluster size (as determined on a 2 × 2 × 2 mm standard template) is shown instead of number of voxels. Numbers in brackets show standard error of the mean.

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Fig. 5. The location of the FFA and VWFA in an individual subject.
(Cohen et al., 2002a, 2002b), while a mirror-symmetric location in the other hemisphere was its right counterpart. Likewise, the right FFA has been reported to have mean coordinates of about (x = −40, y = −55, z = −10) (Kanwisher et al., 1997a, 1997b). When anterior and posterior regions were found, the posterior region was assigned as the FFA.

In each subject, the size of the smaller FFA was fixed at 10 voxels (see Bukowski et al., 2013; Fox et al., 2009; Rossion et al., 2012), for a similar approach) by varying the statistical threshold until 10 voxels were significant on the side with less activation. The same approach was used to identify right and left activation by words in the VWFA. As no data from any given subject can be entered into the analysis unless all 4 regions are identified, this approach allowed us to obtain data from the majority of subjects while allowing an unbiased comparison between the two different localisers (Table 1). We extracted the following information from each of the four identified regions of interest (right and left FFA, right and left VWFA): 1) the peak MR response to each region preferred stimulus (faces in the FFA, words in VWFA); 2) the peak MR response to each regions non-preferred stimulus (faces in the peak voxel of the VWFA, words in the peak voxel of the FFA); and 3) the number of voxels above the contrast threshold within each region.

An alternative to comparing single peak voxels, is to compare the average z-scores across all voxels within each region-of-interest. This yielded similar results to the peak-voxel analysis, and are therefore not reported here for reasons of brevity.

4.4.2. Structurally defined inferior temporal cortex analysis

To examine the relationship between word and face activation in a broader anatomic context, we assessed these in the inferior temporal cortex, using a combined mask of the temporooccipital and posterior divisions of the inferior temporal gyrus (Harvard-Oxford Cortical Structural Atlas; http://www.fmrib.ox.ac.uk/fsl) that was defined at the group level, and transformed back into the individual subject’s native space. In contrast to the strategy used in the functionally defined ROI analysis, all voxels above a set statistical threshold (P < 0.001, uncorrected) were entered into the analysis.

4.5. Statistical analysis

We first examined whether word and face activity was correlated within each hemisphere. Next we calculated a lateralization index, which was the weighted difference (left-right)/(left + right) of hemispheric activation, first for words and then for faces. As such indices can occasionally result in large spurious numbers, values greater than 3 standard deviations from the mean were defined as outliers and removed before statistical analysis. All our analyses were re-done in a secondary analysis that included outliers. These did not change the pattern or significance of the results reported. We chose this lateralization index because it expresses the degree of lateralization essentially as a percentage of the sum amount of activation in both hemispheres; repeating the analyses with a simple difference (left-right) or a ratio (left/right) as alternate lateralization indices did not alter the findings. Our weighted-difference lateralization index results in a positive index corresponding to greater activity on the left and a negative one to greater activity on the right hemisphere. A correlation analysis (Pearson’s r, two-tailed) was performed for the lateralization index of words versus faces.

We performed the above at three levels of analysis, which moved from smaller to larger frames of reference. First, competition may be evident within a functionally defined region. For example, one can ask if, in the right and left FFA, the asymmetry of face activity is inversely correlated with the asymmetry of word activity within these face-responsive regions, which were defined solely by their activity during a face (and not a word) localizer contrast. Similarly, one can then examine if in the right and left VWFA, the asymmetry of word activation is inversely correlated with the asymmetry of face activity within these word-responsive regions. These we called ‘same-ROI’ analyses. These focused solely on MR responses of the peak voxels, as the number of voxels for the non-defining stimulus would be artificially constrained by the use of the other stimulus type to define the region of interest.

Second, one can ask if the lateralization of face activity within functionally defined FFA regions is inversely correlated with the lateralization of word activity within functionally defined VWFA regions. These we called ‘different-ROI’ analyses. The dependent variables for these analyses were both peak MR responses and number of activated voxels.

Third, we examined the lateralization of face and word activity within the broader context of the inferior temporal cortex, whose borders we defined structurally rather than by functional localizers. The dependent variables here were the number of all voxels above the statistical threshold, and the average peak MR response from all clusters of activation.

Other factors may influence the lateralization of both words and faces and mask a complementary relationship between the two. First, to control for a possible influence of handedness, we repeated the analysis but included subjects’ scores on the Edinburgh handedness questionnaire (Oldfield, 1971) as an additional regressor. Second, we reasoned that asymmetry in the available neural resources may also influence the appearance of lateralization of both words and faces. Thus we extracted the grey matter volume and the average cortical thickness of the left and right fusiform gyri. Cortical reconstruction and volumetric segmentation was performed with the Freesurfer image analysis suite, [http://surfer.nmr.mgh.harvard.edu/]. Lateralization indices were calculated for the grey matter volume and the average cortical thickness in the fusiform gyri and entered as additional regressors in the above analyses. All statistical analysis was carried out using R [http://www.R-project.org].

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.brainres.2016.05.009.

References


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