Journal of Experimental Psychology: General
2013, Vol. 142, No. 2, 348–358

0096-3445/13/$12.00 DOI: 10.1037/a0029503

The Joint Development of Hemispheric Lateralization for Words and Faces

Eva M. Dundas, David C. Plaut, and Marlene Behrmann
Carnegie Mellon University

Consistent with long-standing findings from behavioral studies, neuroimaging investigations have identified a region of the inferior temporal cortex that, in adults, shows greater face selectivity in the right than left hemisphere and, conversely, a region that shows greater word selectivity in the left than right hemisphere. What has not been determined is how this pattern of mature hemispheric specialization emerges over the course of development. The present study examines the hemispheric superiority for faces and words in children, young adolescents and adults in a discrimination task in which stimuli are presented briefly in either hemifield. Whereas adults showed the expected left and right visual field superiority for face and word discrimination, respectively, the young adolescents demonstrated only the right-field superiority for words and no field superiority for faces. Although the children's overall accuracy was lower than that of the older groups, like the young adolescents, they exhibited a right visual field superiority for words but no field superiority for faces. Interestingly, the emergence of face lateralization was correlated with reading competence, measured on an independent standardized test, after regressing out age, quantitative reasoning scores, and face discrimination accuracy. Taken together, these findings suggest that the hemispheric organization of face and word recognition do not develop independently and that word lateralization, which emerges earlier, may drive later face lateralization. A theoretical account in which competition for visual representations unfolds over the course of development is proposed to account for the findings.

Keywords: hemispheric specialization, lateralization, face processing, word processing

Extensive behavioral, physiological, and neuropsychological evidence gleaned from investigations with adults reveals the existence of highly specialized and seemingly independent neural mechanisms for visual word recognition in the left hemisphere and for visual face recognition in the right hemisphere (for examples, see Cohen & Dehaene, 2004; Kanwisher, McDermott, & Chun, 1997; for a review, see Toga & Thompson, 2003). Although this lateralization profile is robust and consistent across studies, what remains unclear is the developmental trajectories that give rise to these patterns of specialization, and whether these trajectories—and perhaps the resulting adult mechanisms—are as independent as commonly thought.

The present article reports the results of a visual discrimination task with lateralized presentation of words and faces, conducted with right-handed individuals ranging from 7 to 29 years of age. Our goal was twofold. First, we evaluated the developmental emergence of cerebral asymmetries for word and face recognition. Second, we examined the relationship between face processing and word processing within individual to determine whether development in these two domains evolves entirely independently or whether there is some relationship between their patterns of emergence.

The Development of Word Lateralization

The superiority of the left hemisphere for visual word processing in adults is well established (for reviews, see Grüsser & Landis, 1991; Hellige, Laeng, & Michimata, 2010). Typically, in such studies, performance is better when orthographic stimuli are presented to the right (RVF) than left visual field (LVF). Consistent with this, imaging studies with adults have documented a region in the left hemisphere—the visual word form area (VWFA; Talairach coordinates: $x = -43$, $y = -54$, $z = -12$) — that is selectively activated for words over other stimulus types (Cohen et al., 2000; Puce, Allison, Asgari, Gore, & McCarthy, 1996; for a review, see Price & Devlin, 2011). Similarly, event-related potential (ERP) studies have uncovered a left lateralized N170 that is differentially amplified for words compared with other visual stimuli (for recent examples, see Maurer, Rossion, & McCandliss, 2008; Mercure, Cohen Kadosh, & Johnson, 2011).

Developmentally, the selective activation of the VWFA in the left hemisphere is not evident in young children, and an adult pattern of lateralization emerges at or around 10 years of age

---

Eva M. Dundas, David C. Plaut, and Marlene Behrmann, Department of Psychology, Carnegie Mellon University.

This research was supported by National Institutes of Health (B-squared) Training Grant T32GM081760 awarded to Eva M. Dundas, National Science Foundation (NSF) Grant BCS0923763 awarded to Marlene Behrmann and David C. Plaut, and NSF Science of Learning Center Grant (SBE-0542013 to the Temporal Dynamics of Learning Center) awarded to Marlene Behrmann. We thank the administrators and parents of the Community Day School in Pittsburgh for their cooperation and permission to test the students. We also thank Mayu Nishimura for her helpful comments on the manuscript and Lauren Lorenzi for her assistance with data collection.

Correspondence concerning this article should be addressed to Eva M. Dundas, Department of Psychology, Carnegie Mellon University, Pittsburgh, PA 15213-3890. E-mail: edundas@andrew.cmu.edu or plaut@cmu.edu or behrmann@cmu.edu

(Schlaggar & McCandliss, 2007; Turkeltaub, Flowers, Lyon, & Eden, 2008). This maturational pattern is also evident in ERP studies that show that the differential neural response to words emerges roughly a year and a half of reading instruction (Maurer, Brandeis, & McCandliss, 2005; Maurer, Brem, Bucher, & Brandeis, 2005) and shows some evidence of left lateralization between 7 and 10 years of age, although perhaps still not to the same degree observed in adult patterns (Posner & McCandliss, 1999; Schlaggar et al., 2002). That the asymmetry for word processing requires considerable ontogenetic time to emerge is perhaps unsurprising given that, on an evolutionary time scale, reading is a relatively recent cultural invention and, hence, no innate mechanism for orthographic processing is likely to exist. Instead, typically developing children require years of overt training and extensive practice to learn to read fluently, and the adult pattern of hemispheric lateralization appears to emerge in tandem with increasing reading proficiency (Marcel, Katz, & Smith, 1974).

The finding that the selective activation of the VWFA is experience-dependent is not only apparent in young readers; the strength and lateralization of the VWFA increases with experience in adult second-language learners as well, suggesting a fine-tuning of the system over the course of familiarity with a particular orthography (Baker et al., 2007; Wong et al., 2011). Taken together, these data suggest that a protracted period of experience is necessary before the hemispheric superiority for words becomes evident.

Development of Face Lateralization

Given the critical social and evolutionary importance of faces and the extensive exposure to faces from birth, one might expect that the face recognition system would achieve adult levels of performance and hemispheric organization early in development, and certainly in advance of the word recognition system. Interestingly, however, this is not so, and adult levels of performance are not yet evident when 10-year-olds perform identity matching of faces differing in the spacing between the features (Mondloch, Robbins, & Maurer, 2010). Furthermore, children continue to show large improvements in their recognition of unfamiliar faces until about 12 years of age, in contrast with their adult levels of performance in recognizing unfamiliar houses (Diamond & Carey, 1977) and shoes (Teunisse & de Gelder, 2003). In fact, substantial improvements in face recognition abilities, as measured by the Cambridge Face Memory Test, continue to occur from childhood (ages 9–12) into young adulthood (ages 18–29 years) (O'Hearn, Schroer, Minshew, & Luna, 2010), with peak performance sometimes still not evident until approximately 30 years of age (Germine, Duchaine, & Nakayama, 2011).

Consistent with this protracted development of face perception abilities, the emergence of the adult neural organization for faces is also delayed. In adults, an area in the right inferior temporal cortex, termed the *fusiform face area* (FFA; Talairach coordinates: $x = 40$, $y = -55$, $z = -10$), responds more strongly to images of upright faces compared with inverted faces or other nonface objects (for examples, see Kanwisher, 2000; Kanwisher et al., 1997; Sergent, Ohta, & MacDonald, 1992; Sergent, Signoret, & Rolls, 1992; Spiridon, Fischl, & Kanwisher, 2006; Yovel & Kanwisher, 2005), and similar findings are observed using ERP recording (for examples, see Allison, Puce, Spencer, & McCarthy, 1999; Rossion, Joyce, Cottrell, & Tarr, 2003).

Selective activation of the FFA for faces is 3 times smaller in children than in adults (Golarai et al., 2007) and emerges slowly through childhood and adolescence (Cohen Kadosh, Cohen Kadosh, Dick, & Johnson, 2010; Gathers, Bhatt, Corbly, Farley, & Joseph, 2004; Joseph, Gathers, & Bhatt, 2011; Scherf, Behrmann, Humphreys, & Luna, 2007). Although some face selectivity may be apparent in the right but not left fusiform gyrus as early as 4–5 years of age (faces vs. shoes; Cantlon, Pinel, Dehaene, & Pelphrey, 2011), the laterality pattern is still far from adultlike in 5- to 8-year-olds (Scherf et al., 2007) and is not stable until early adolescence (12–14 years; Aylward et al., 2005).

The Relationship Between Word and Face Processing

In the absence of any apparent relationship between face and word processing, a natural assumption is that the observed similarities in the emergence of their neural organization and performance are coincidental and that the two domains develop independently of each other, perhaps as a result of brain maturation and/or experience. Some researchers, however, have proposed that these domains are not fully independent. For example, Phippard (1977) found that deaf individuals who do not use verbal communication do not demonstrate an LVF advantage for faces, suggesting, counterintuitively, that a lack of auditory input plays a role in the lateralization of face processing. More recently, Dehaene et al. (2010) showed that adults with no formal education in reading have heightened left hemisphere activation to faces, compared with literate controls, and that formal instruction in reading subsequently decreased the left fusiform activation to faces. Similarly, young children show decreasing responses to faces in the left fusiform (VWFA) with increasing letter knowledge (Cantlon et al., 2011), a point we return to in detail in the Discussion section.

To be clear, the coincidental account of parallel systems and matching developmental trajectories can never be ruled out, but if a systematic relationship can be established between the developmental patterns in the two domains—particularly if it can be given a well-motivated, mechanistic account—then the coincidental account becomes far less plausible. Here, we systematically analyze the developmental emergence of the lateralization of words and faces and their relationship across a large age span from young childhood through adulthood. To foreshadow the results, we find a systematic relationship between the emergence of face and word lateralization—face lateralization occurs at a later stage than word lateralization, and its extent is predicted by reading skill. These results are consistent with a recent mechanistic proposal in which the mechanisms supporting word and face representations compete for common neural resources. However, by virtue of the pressure for fine-grained visual representations to be in close proximity to language representations to subserve word recognition, the left hemisphere word bias emerges first (Plaut & Behrmann, 2011). This earlier language-biased left hemisphere lateralization for words drives a later right hemisphere lateralization for faces.

Method

Participants

Participants were typically developing monolingual native English speakers. The child group consisted of 24 children aged 7.53–9.36 years (*M* = 8.4 years, *SD* = 0.67 years; 11 males and 13 females). The young adolescent group consisted of 24 participants aged 11.08–13.29 years (*M* = 12.2 years, *SD* = 0.73 years; 11 males and 13 females). The participants in these two groups were recruited from a local school, and parents signed consent forms to allow the minor's participation. On the basis of consultation with the school, we excluded any participant with any cognitive and/or social impairment. The 24 adult participants aged 17–29 years (*M* = 21.5 years, *SD* = 3 years; 10 males, 14 females), recruited from the subject pools at Carnegie Mellon University, provided informed consent to participate.

All participants had normal or corrected-to-normal vision. There was no significant difference across the three groups in handedness, as determined by their scores on the Edinburgh Handedness Inventory (Oldfield, 1971; *M*s: adults −83.2; adolescents −84.8; youngest group −85.3; one-way analysis of variance [ANOVA], *ns*). We note that some items from this inventory were excluded as inappropriate for younger children (e.g., striking a match), but this does not affect the laterality indices (as they are simply calculated as a function of number of items completed). Scores of reading comprehension and quantitative reasoning from the standardized Education Records Bureau (ERB) exam were obtained for 20 of the children and 23 of the adolescents. The reading comprehension section consisted of short passages of text with questions on the main idea, supporting ideas, vocabulary, and possible inferences.

Stimuli

Thirty male and 30 female face images obtained from the Face-Place Database Project (Tarr, 2008) were used in this experiment. All faces were forward facing with neutral expression (see example in Figure 1). The faces were cropped to remove hair cues and presented in grayscale against a black background. Stimuli were 1.5 in. in height and 1 in. in width, yielding visual angles of 4.8° and 3.2°, respectively. On each trial, the pair of faces matched on gender.

The word stimuli consisted of 60 four-letter words (30 pairs), presented in gray Arial 18-point font against a black background. Stimuli were approximately 1/2 in. in height and 1 in. in width, yielding visual angles of 1.6° and 3.2°, respectively. Pairs were matched so that the words differed by one of the interior letters; half the pairs differed in the second letter and the other half differed in the third letter (see example in Figure 1).

Although our primary focus was on words and faces, we also adopted a third visual category, that of cars, to serve as a control stimulus class. The 60-car stimuli were presented in gray scale at a three fourths left-front facing view. Stimuli were approximately 1.75 in. in width and 1 in. in height, yielding visual angles of 5.57° and 3.2°, respectively (see example in Figure 1).

Procedure

The experiment was run on a laptop computer using E-prime software (Schneider, Eschman, & Zuccolotto, 2002). Participants sat approximately 18 in. from the screen. Words, faces, and cars were presented in separate, counterbalanced blocks of trials. Participants viewed a central fixation cross whose duration ranged

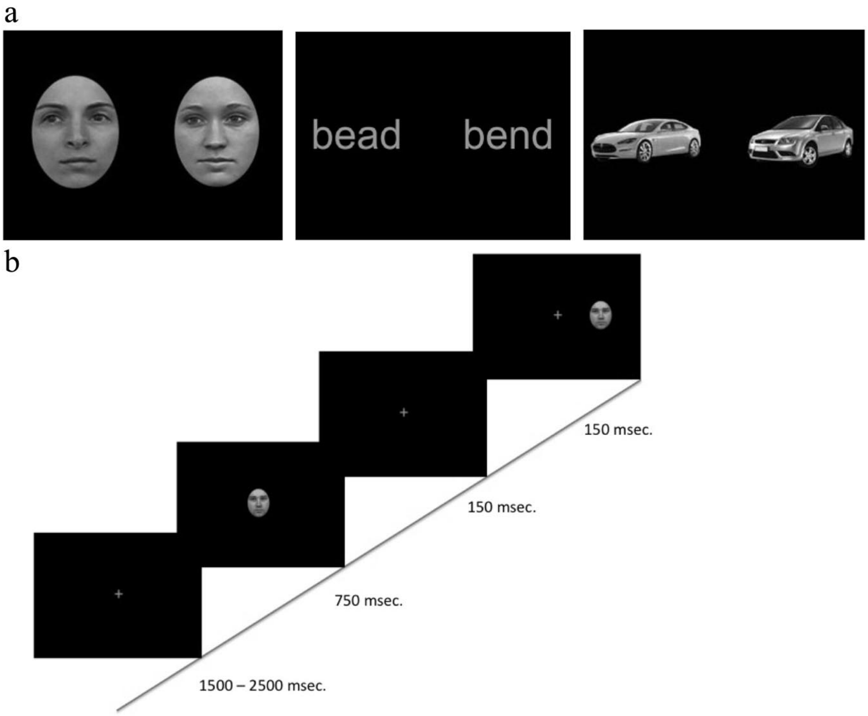

Figure 1. a. Example of a pair of faces, words, and cars used in half-field experiment. b. Illustration of the temporal sequence of an individual trial (with faces, words, and cars appearing in separate blocks).

between 1,500 and 2,500 ms. Following the offset of the fixation cross, a centrally presented (word, face, or car) stimulus appeared for 750 ms and was followed immediately by a second stimulus of the same type (word, face, or car) presented for 150 ms in either the LVF or the RVF. The center of the lateralized stimulus was 5.3° from fixation. Participants were instructed to keep their gaze fixated centrally throughout the experiment and to respond by pressing one of two buttons to indicate whether the second stimulus was identical to the first or not (same–different judgment). The fixation cross appeared following the button press and indicated the start of the next trial. The presentation of stimuli in the LVF and RVF was randomized per subject with equiprobable presentation in each field within a block. For all classes of stimuli, there were 96 trials, which were split into three mini blocks to give participants time to rest in between blocks.

Children and young adolescents were tested in groups of two to four (each on a separate laptop but with the identical protocol) in a quiet room in the library of their school. Adults were tested individually in a quiet room at Carnegie Mellon University.

Results

The design of the experiment entailed a between-subjects variable of age (children, young adolescents, adults) with two within-subject factors: field (left, right) and stimulus type (word, face, cars). The focus of this study was on the patterns of lateralization of faces and words as a function of age, and we examine these results first. To ensure that our findings were specific to faces and words, we included cars as a control visual class.

Although both accuracy and reaction time (RT) data were collected, the stimulus exposure duration was time-limited (to preclude saccades), and, under such conditions, accuracy is usually the more informative measure. For completeness, we also conducted the same analyses using RT. Because we sampled three specific age groups, rather than sampling uniformly across the age span, we first conduct ANOVAs with age as a between-subjects variable, but we also report regression analyses including age as a continuous variable.

With accuracy as the dependent measure, a 3 × 3 × 2 (Age Group × Stimulus Type × Visual Field) ANOVA revealed a main effect of stimulus type, $F(2, 69) = 27.53$, $p < .001$, that was driven by higher accuracy across all groups for the cars. The same was true in an ANOVA using RT in which there was a significant main effect of stimulus type, with faster RT for cars across all groups, $F(2, 69) = 4.61$, $p = .012$. Because performance on cars was not well matched with that of words and faces (even though we attempted a priori to match on some image properties), as is described below, and cars serve as a control stimulus type (as our main conceptual interest is in comparing faces and words), we conducted the analyses of the car condition separate from that of faces and words and report the analyses after our main comparisons.

Lateralization of Visual Processing of Words and Faces

With accuracy as the dependent measure, a 3 × 2 × 2 (Age Group × Words/Faces Stimulus Type × Left/Right Visual Field) ANOVA revealed a marginally significant three-way interaction, $F(2, 69) = 2.43$, $p = .096$, $\eta_p^2 = .07$. There was, however, a highly significant two-way interaction between stimulus type and visual field, $F(2, 69) = 26.11$, $p < .001$, due to the superior accuracy for faces in the LVF over the RVF, $t(71) = 2.38$, $p = .020$, and for words in the RVF over LVF, $t(71) = -5.04$, $p < .001$. This interaction confirms the expected hemispheric asymmetry for words and faces. There were no main effects of stimulus type or field, nor any other significant interactions. There was, however, a significant main effect of age group, $F(2, 69) = 15.8$, $p < .001$, $\eta_p^2 = .31$. Post hoc comparisons using Tukey's honestly significant difference test (with $p < .05$) indicated a significant difference in mean accuracy between the adult and child group (mean difference = .096, $p < .001$) and between the young adolescent and child group (mean difference = .110, $p < .001$). No significant differences were found between the accuracy scores of the adult and adolescent groups.

With RT as the dependent measure, the same 3 × 2 × 2 did not yield a significant three-way interaction, $F(2, 69) = 0.467$, $p = .629$, nor any two-way interactions. The only significant main effect was of group, $F(2, 69) = 15.62$, $p < .001$; whereas the adults and young adolescents responded equally fast (698.6 ms and 696.02 ms), the child group responded significantly more slowly than both (1095.6 ms). This rank ordering of children as being distinct from the other two groups, which did not differ from each other, mirrors the main effect of group in accuracy.

In light of the marginally significant three-way interaction of accuracy and our a priori interest in the differential effects of hemispheric superiority across the age groups, we explored the pattern of stimulus type and field effects within each age group.

Within-group analyses

Adult group analyses. An ANOVA of the data from the adult group, using stimulus type and visual field as within-subject variables and accuracy as the dependent measure, revealed a significant two-way interaction, $F(1, 23) = 42.0$, $p < .001$, $\eta_p^2 = .65$. As evident from Figure 2a, this interaction is driven by significantly higher accuracy for words presented in the RVF over the LVF, $t(23) = 3.47$, $p = .002$, and significantly higher accuracy for faces presented in the LVF over the RVF, $t(23) = 4.79$, $p < .001$. There was no significant difference between accuracy for face and words presented in their "preferred" field (i.e., faces in LVF and words in RVF, respectively), $t(23) = 0.314$, $p = .757$. This result replicates the standard pattern of hemispheric specializations of faces and words in the mature brain, as expected from the extensive literature on cerebral asymmetries. The results also show equal accuracy for faces and for words in their preferred hemispheres.

Young adolescent group analyses. The same ANOVA applied to the data from the adolescents also revealed a significant interaction of Stimulus Type × Visual Field, $F(1, 23) = 6.14$, $p = .059$, $\eta_p^2 = .146$. As displayed in Figure 2b, this group showed significantly higher accuracy for words presented in the RVF over those in the LVF, $t(23) = 3.37$, $p = .003$; however, there was no significant difference in accuracy for faces across the LVF and RVF, $t(23) = 0.24$, $p = .810$. This pattern reflects only one half of the adultlike pattern of hemispheric asymmetry, with clear specialization for words in the left hemisphere but no hemispheric specialization for faces.

Child group analyses. The same ANOVA conducted on the data from the child group revealed only a very weak trend toward an interaction of Stimulus × Visual Field, $F(1, 23) = 2.78$, $p =$

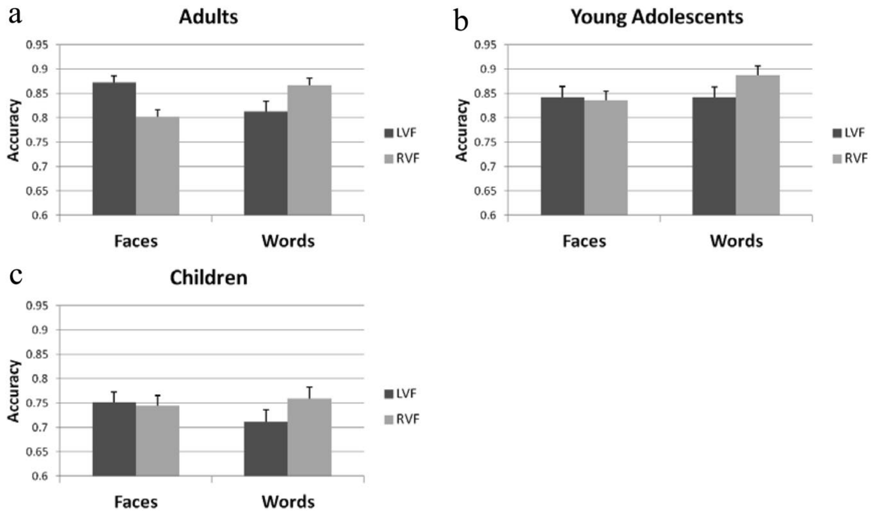

Figure 2. Mean accuracy and ± 1 *SE* for (a) adults, (b) young adolescents, and (c) children as a function of stimulus type for the left and right visual field presentation. LVF = left visual field; RVF = right visual field.

.094, $\eta_p^2 = .12$. Even so, given our particular interests, we conducted the planned post hoc *t* tests. These revealed that accuracy was significantly higher for words presented in the RVF over LVF, $t(23) = 2.25$, $p = .034$, but that there was no difference in accuracy for faces across the two visual fields, $t(23) = 0.342$, $p = .735$ (see Figure 2c). There were no apparent differences in accuracy between words and faces presented in the respective "preferred" fields, $t(23) = -0.455$, $p = .654$. In sum, these findings are consistent with the pattern of the young adolescents with a field difference evident for words but not for faces.

Relationship between word and face processing. To examine the relationship among these age-related effects of visual field biases in a more continuous fashion, as well as the relationship between the bias for words and for faces, we performed a regression analysis on the magnitude of the face and of the word-hemispheric superiority across all participants. A linear regression revealed a small but significant effect of age on the degree of face lateralization (dependent measure is difference score: LVF accuracy – RVF accuracy: $R^2 = .112$), $t(1, 70) = 2.97$, $p = .004$, so that, for every year in age, there was a mean increase in face lateralization accuracy of .006 (see Figure 3a). Consistent with the word lateralization data from the ANOVAs reported above, the linear regression did not reveal a significant effect of age on the degree of word lateralization (dependent measure is difference score: RVF accuracy – LVF accuracy: $R^2 = .014$), $t(1, 70) = 0.038$, $p = .970$, as shown in Figure 3b. Although there was no significant difference between the regression coefficient for face lateralization and age and the regression coefficient for word lateralization and age ($Z = .58$, $p = .56$), the difference scores between word and face lateralization were correlated with age ($R^2 = .065$), $t(1, 70) = 2.21$, $p = .03$.

As we had expected to observe a correlation between the lateralization of faces and the lateralization of words and did not, $r(72) = -.02$, $p = .865$, we examined whether performance on a different, more extensive reading test, with greater discriminability across age, might better predict the emergence of face lateralization. Unsurprisingly, for the same reason as above, there was no significant relationship between reading comprehension percentile rank on the ERB examination and word lateralization for the child and young adolescent groups ($R^2 = .013$), $t(1, 41) = -0.726$, $p = .427$. Especially revealing, then, is that the exact same analysis with ERB reading skill pitted against face lateralization in the children and young adolescent groups revealed a significant correlation ($R^2 = .153$), $t(1, 41) = 2.71$, $p = .010$, and this was true even after regressing out age, overall accuracy of face discrimination, and percentile rank on the quantitative reasoning section of the ERB examination ($R^2 = .156$), $t(1, 41) = 2.72$, $p = .01$ (see Figure 4). This association between standardized reading performance and the magnitude of face lateralization was evident within the child group alone ($R^2 = .305$), $t(1, 18) = 2.81$, $p = .012$, and was marginally significant when analyzing the adolescent group data alone ($R^2 = .128$), $t(1, 21) = 1.75$, $p = .094$.

Lateralization of Visual Processing of Cars

In the following analyses, we determine whether a category other than faces shows the same relation with visual processing lateralization and reading development. For example, it might be the case that many visual categories (houses, numbers, tools, abstract shapes, cars, etc.) would show decreased processing in the RVF and left hemisphere as children learn to read. To assess this, we examined the lateralization of accuracy and RT to car stimuli in the same individuals and also evaluated whether any laterality effects are associated with reading proficiency, measured independently.

A 3 × 2 (Age Group × Visual Field) ANOVA on cars alone using accuracy as the dependent measure did not reveal a significant two-way interaction, $F(1, 69) = 1.16$, $p = .319$, indicating the absence of hemispheric asymmetries for making same/different decisions on cars. There was, however, a significant main effect of group, $F(2, 69) = 4.18$, $p = .019$, with the child group performing less accurately than the other two groups. The same ANOVA with RT as the dependent measure also did not reveal a significant interaction of Age × Field, $F(1, 69) = 0.317$, $p = .729$, but also

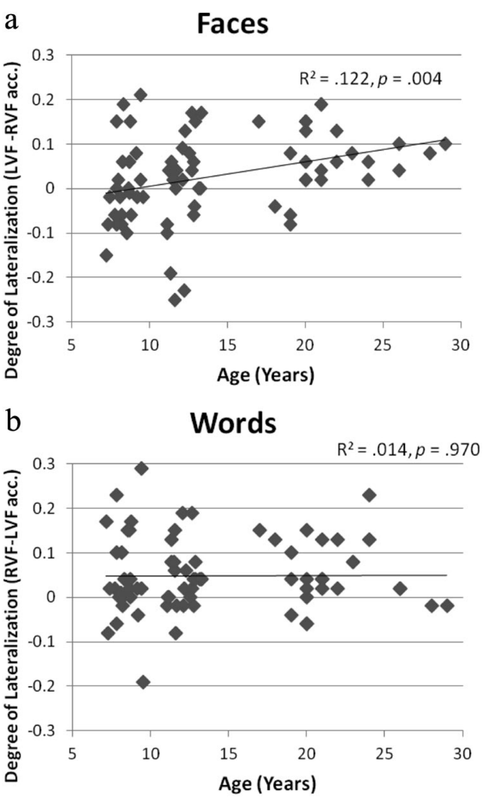

Figure 3. Scatterplot with correlation analysis showing relationship between age in years and (a) lateralization (LVF−RVF) for faces and (b) lateralization (RVF−LVF) for words. LVF = left visual field; RVF = right visual field; acc. = accuracy.

showed a main effect of group, $F(2, 69) = 26.40$, $p < .001$, with children being significantly slower than the other two groups.

Additionally, a linear regression did not show a significant effect of age on the degree of lateralization (computed as RVF−LVF in accuracy) for cars, ($R^2 = .014$), $t(1, 70) = 0.156$, $p = .877$. Unsurprisingly, a regression analysis with ERB reading score and degree of lateralization showed no significant association between these measures ($R^2 = .01$), $t(1, 41) = 0.651$, $p = .519$.

Discussion

There is a large body of evidence supporting the claim that there are separate, specialized mechanisms in the adult brain for processing faces and words, in the right and left hemispheres, respectively. In the present study, we explored the developmental pattern by which these hemispheric specializations arise and, further, examined whether these specialized systems are as categorical and independent as commonly thought. Although previous studies have investigated the development of either word or face processing, few have specifically investigated them jointly and assessed the possibility of a relationship between them. Here, we examined hemispheric superiorities in individuals aged 7–29 years in a matching task using face and word stimuli that were carefully selected and well matched (see Figure 1b). To ensure that our findings were specific to faces and words, we also assessed hemispheric superiorities for another visual class, that of cars, using the same half-field-matching paradigm.

The data from the adult participants replicated the well-established pattern of hemispheric lateralization (Iaccino, 1993) with more accurate word processing in the RVF than LVF, and, conversely, more accurate face processing in the LVF than RVF. Although overall accuracy did not differ between the young adolescents and adults, their pattern of laterality did: Whereas both groups evinced the RVF superiority for word processing, unlike the adults, the young adolescents showed no hemifield advantage for faces. This replicates a similar finding reported previously (Marcel et al., 1974). The child group performed less accurately overall than either of the older groups but, intriguingly, demonstrated the same pattern of lateralization seen in the young adolescent group: an advantage for words in the RVF and no hemifield advantage for faces.

Although age did not account for any of the variance when pitted against the hemifield difference (RVF−LVF advantage) for words, there was a significant relationship between age and degree of face lateralization (difference score: LVF−RVF), reflecting the evolving developmental nature of face selectivity. Finally, the magnitude of face lateralization, but not of word lateralization, was predicted from an individual's performance on a sensitive, standardized reading test, even after regressing out age, face-processing accuracy, and quantitative reasoning scores.

Importantly, we show that that this last result (hemispheric specialization for faces is related to reading proficiency) is specific to the relationship between faces and words. Using car stimuli as a control condition, we observed no hemispheric specialization for cars and, moreover, no relationship between the visual processing of cars and reading proficiency. That we see specificity in the relationship between the lateralization for faces and reading proficiency constrains the account we offer for the emergence of hemispheric superiorities for face and word processing.

Before turning to this account, it is interesting to note that a particular level of accuracy is not critical for the emergence of hemispheric specialization: Laterality effects are essentially independent of accuracy. Whereas the young adolescents performed as accurately as the adults for both stimulus classes, the two groups

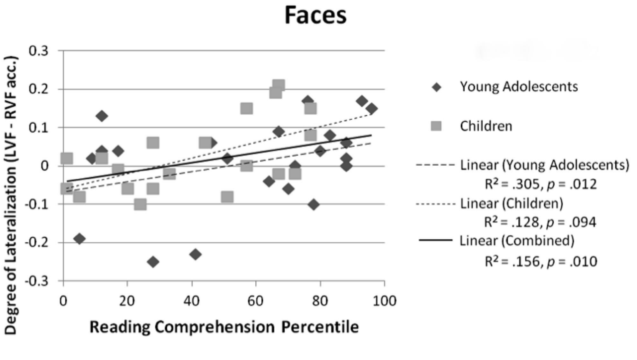

Figure 4. Scatterplot and correlation analysis showing significant relationship between reading comprehension percentile (on the standardized Education Records Bureau examination) and face lateralization (LVF−RVF) for the young adolescents, children, and for the two groups in combination. LVF = left visual field; RVF = right visual field; acc. = accuracy.

differed in their patterns of lateralization (words vs. faces). Furthermore, the children performed more poorly than either of these groups across both stimulus classes but showed the same pattern of lateralization as the young adolescents for both words and faces, and as the adults for words. Thus, it appears that a threshold of perceptual competence is not a necessary prerequisite for the onset of hemispheric superiority.

Development of Hemispheric Specialization for Words and for Faces

Our finding that a hemispheric superiority for word processing is evident in young children is consistent with data showing that children begin evincing lateralization for word processing early on in the course of learning to read (Marcel et al., 1974; for a review, see Schlaggar & McCandliss, 2007). Interestingly, the extent of the lateralization (but not absolute accuracy levels), at least on a sequential discrimination task such as that used here, is not associated with age. It does remain possible that a more graded pattern of word lateralization may be apparent in children younger than our participants—the youngest children in our sample are roughly 7 years of age. Examining similar hemispheric effects in younger children or less competent readers, independent of absolute age, would be highly informative in terms of the evolving lateralization of word processing.

Unlike the hemispheric word bias, our results suggest that the developmental timing of the lateralized bias for faces is considerably delayed. These findings are consistent with several recent studies demonstrating the protracted developmental time course to achieve adult levels of face perception (Carey & Diamond, 1980; Diamond & Carey, 1977; Diamond, Carey, & Back, 1983; Ellis, Shepherd, & Bruce, 1973; Flin, 1985; Mondloch, Dobson, Parsons, & Maurer, 2004; O'Hearn et al., 2010) and with recent functional imaging studies indicating that young children do not consistently activate the FFA (Aylward et al., 2005; Gathers et al., 2004; Golarai et al., 2007; Joseph et al., 2011; Passarotti, Smith, DeLano, & Huang, 2007; Passarotti et al., 2003; Peelen, Glaser, Vuilleumier, & Eliez, 2009; Scherf et al., 2007; for a recent review, see Scherf, Behrmann, & Dahl, 2012). Taken together, the prolonged acquisition of behavioral skills and delayed functional activation for faces observed in children, and even in adolescents, compared with adults, is compatible with the present results in which the hemispheric superiority for faces is not yet fully mature.

Independence of Face and Word Lateralization?

Although the developmental patterns we observe for word and face processing line up with those reported previously, the key issue is whether these patterns are related in any way. Perhaps the most critical and counterintuitive aspect of our data, then, is that, despite the evolutionary importance of face recognition and the earlier exposure to faces compared with words, it is the word system that achieves mature hemispheric organization—at least in terms of lateralization—far earlier than the face system. Apparently, the substantial experience with faces in childhood and the developmental improvement in face recognition do not provide sufficient pressure to drive hemispheric specialization. Rather, word lateralization precedes that of face lateralization, and the reading comprehension scores predicts the degree of face lateralization. Taken together, these data suggest that lateralization of face-processing mechanisms is not independent of the lateralization of visual word-processing mechanisms.

Indeed, important evidence to support the idea that the development of face and word selectivity share some relationship comes from a recent study by Cantlon et al. (2011) in which they demonstrated that young children show decreasing responses to faces in the left fusiform (VWFA) with increasing letter knowledge, and, as we argue below, this leads to the later instantiation of right lateralization for face processing. Of interest too is that it is only face stimuli that showed decreased representation in the left fusiform as children learn about letters, but activation for other stimuli (shoes) were not affected. The absence of any relationship between car and face/word performance and lateralization in the present study is entirely compatible with the absence of an effect of shoes on letter/face representations in the Cantlon et al. (2011) study.

How Might These Seemingly Independent Systems Be Mechanistically Related?

Given that there is some yoking between reading proficiency and the changes in face processing, revealed here in the lateralization findings, the key questions concern the mechanism by which this yoked relationship plays out. Plaut and Behrmann (2011) have recently instantiated a computational description of this mechanism in which they have considered the relative contributions of the left and right hemispheres for face and word processing, as well as the emergent topographic organization within an individual. On this account, because both words and faces place distinctive demands on high-acuity vision, words and faces compete for representational space in both hemispheres, and this competition takes place specifically in that cortical subarea adjacent to regions of retinotopic cortex encoding information from central vision with maximal discriminability (Hasson, Levy, Behrmann, Hendler, & Malach, 2002; Levy, Hasson, Avidan, Hendler, & Malach, 2001), notably the VWFA and the FFA. To minimize connection length (and the opportunity for errors to arise as signal propagation distance increases or interhemispheric engagement is necessary), orthographic representations are further constrained to be proximal to language-related information, which is left-lateralized in most individuals. As a result, words (and, presumably, letters before that) gradually come to rely most heavily (albeit not exclusively; see right hemisphere accuracy for word discrimination in Figure 2) on the left fusiform region (VWFA) as an intermediate cortical region bridging between early vision and language. This idea is also consistent with the interactive view that left occipitotemporal regions become specialized for word processing because of top-down predictions from the language system integrating with bottom-up visual inputs (Devlin, Jamison, Gonnerman, & Matthews, 2006; Kherif, Josse, & Price, 2011; Price & Devlin, 2011; Twomey, Kawabata Duncan, Price, & Devlin, 2011). Interestingly, recent research on perceptual narrowing in infants also appeals to the influence of language on face perception with the observation that silent articulation during face perception may enhance perceptual skill (Patterson & Werker, 2002).

Because of the competition of face representations with word representations, face representations consequently become mostly lateralized to the right fusiform region (FFA) (albeit not exclusively; see left hemisphere accuracy for face discrimination in Figure 2). Note that although the system for face processing may be undergoing refinement with development, the hypothesis is that it is only when reading co-opts the left hemisphere that the pressure for hemispheric specialization begins and thus triggers the lateralization of face processing. Plaut and Behrmann (2011) offered support for this view by demonstrating, within the context of the computational simulation, the acquired anatomic localization and the evolving hemispheric specialization of both words and faces. The empirical data reported here fit nicely with this model, which provides a developmental account for why face lateralization is not present initially, and why it does not emerge simultaneously with word lateralization; additionally, this model, as is also true of the empirical data, evinces a gradual shift to the right hemisphere in relation to continuing improvements in reading ability.

The account offered by Plaut and Behrmann (2011) is generally compatible with the Dehaene and Cohen's "recycling" hypothesis (for a review, see Dehaene & Cohen 2011) but also diverges from it in some respects. Dehaene and colleagues propose that, because orthographic representations have not been present long enough culturally to have evolved dedicated processing mechanisms, the hemispheric specialization for words comes from a "recycling" of a cortical area devoted to processing information with similar visual constraints (i.e., faces). Thus, like Plaut and Behrmann, they propose that the development of the visual word form area is yoked to changes in face processing, and they also recognize the top-down influences on the lateralization of visual word processing from language-related processing. As in the Cantlon et al. (2011) article, on this recycling account, the refinement of the left hemisphere results in the pruning back of neural responses for nonpreferred categories (such as faces), and so the phylogenetic recycling and ontogenetic reorganization have similar ultimate outcomes for neural organization.

One last point is that the framework offered by Price and colleagues (Price & Devlin, 2011; Seghier & Price 2011) suggests that the initiation of hemispheric specialization does not start with the left hemisphere but rather that the left lateralization for words results from decreased activation for words in the right hemisphere, a direct consequence of reduced reliance on language support in that hemisphere. Whether the initial trigger is left- or right hemisphere determined may thus require further consideration and future investigation.

Relation to Other Accounts of Hemispheric Specialization

We have offered an account of the developmental pressures that drive hemispheric differences for visual discrimination of complex visual patterns (words and faces). Numerous other proposals of lateralization effects have been offered, too, although most, if not all, focus on fundamental or intrinsic differences between the hemispheres. For example, it has been suggested that the two hemispheres are differentially sensitive to different spatial frequencies (Robertson & Ivry, 2000) or that the hemispheres have a differential predisposition to process inputs categorically versus by coordinate relations (Kosslyn et al., 1989). A further possibility is that the right hemisphere mediates more configural or holistic processing, whereas the left hemisphere undertakes more analytical processing (see also Farah, 2000, for discussion of a two-stream system, one for faces and one for words). These characterizations of the two hemispheres are not mutually exclusive with one another, nor with the account we have proposed. Indeed, both faces and words require high-spatial frequency information for discrimination between similar exemplars, and both words and faces are recognized by processing both parts and the whole, and the extent to which this is so may be a function of experience (de Heering & Rossion, 2008). Just as the letters are parts of a word, so the eyes/nose/mouth are parts of a face, and just as faces are processed configurally, good readers process letters in parallel. Thus, even if the hemispheres had inherently different spatial frequency and/or configural competence, it is not obvious that this is the initial mechanism that drives the hemispheric superiorities for the two stimulus types.

Potential Limitations

Before concluding, we need to consider a few final issues. The first concerns a potential confound in our data regarding differences in the ability to maintain fixation as a function of age. One possible alternative explanation for our data may be that the children are not as good at fixating as is the case for the older groups. We do not think this a plausible alternative for several reasons. First, the experimental paradigm is optimized to ensure central fixation (brief exposure duration, equiprobable sampling of left and right field in a mixed block of trials). Second, and more relevant, is that the differential pattern across age holds only for faces and not for words—it seems highly unlikely that the children would show fixation differences for one condition but not the other. Although the lower accuracy overall in the children might potentially be explained by poorer fixation stability (but also by their young age), the differential profile for words and faces cannot obviously be accommodated by this interpretation.

A second issue that warrants some discussion is whether the results we report are specifically a function of the task we adopted (same–different matching), in which case they may not be applicable more generally. Although we do not have converging data from a different task, we are encouraged by the fact that other studies report data consistent with ours (e.g., Cantlon et al., 2011, using shoes, faces, letters, numbers, and scrambled stimuli). Additionally, our data are consistent with the Cantlon et al. (2011) finding in that we did not find a change in hemispheric lateralization for nonface stimuli (i.e., cars) using the same–different matching paradigm. Whether the patterns we report really hold across all possible tasks remains to be definitively determined, of course, but there seems to be no a priori principled reason why this would not be the case.

Finally, the last remaining issue concerns the relationship between the research described here and the face perception findings that come from the study of infant perception. One possible point of discrepancy lies in the fact that some studies have reported that there is a right hemisphere advantage for face processing even in infants. For example, infants aged between 18 and 42 weeks can discriminate between their mother and a stranger's face better in the right than left field (de Schonen & Mathivet, 1990), and early deprivation of visual input to the right hemisphere severely impairs the development of expert face processing, whereas deprivation restricted mainly to the left hemisphere does not (Le Grand, Mondloch, Maurer, & Brent, 2003). Infants also demonstrate a leftward gaze bias when viewing faces (Guo, Meints, Hall, Hall, & Mills, 2009). Whether these hemispheric differences/biases are prewired or emerge from, for example, infants looking at the caregiver through the LVF (on carrier's left side, leaving the usually dominant right hand free) remain controversial. Also, these early biases might reflect a foundational aspect of hemispheric difference (e.g., differential sensitivity to spatial frequency) as discussed above. Thus, this differential field/hemisphere sensitivity might not be directly related to the topographic organization of words and faces but may serve as an early biasing signal that becomes further tuned with experience and is eventually co-opted for mature face processing. Note, too, that this early bias does not seem to coincide with a mature right hemisphere FFA given the consistent findings that this neural region is not mature for roughly the first decade of life, and a lesion to either hemisphere early in childhood adversely impacts face perception to an equivalent degree. In light of this, the necessity and sufficiency of these early biases remain to be explored (de Schonen, Mancini, Camps, Maes, & Laurent, 2005), and the relationship between these biases and the adultlike behavioral and neural signatures, however, clearly requires further investigation.

Conclusions

In conclusion, our data show that hemispheric specialization for words develops prior to hemispheric specialization for faces, with face lateralization being related to reading comprehension ability. These results fit well with a model in which word processing becomes left lateralized because of the pressure to be proximal to language areas, and that, subsequently, by means of competition for representational space in the left fusiform gyrus, face processing becomes lateralized to the right fusiform homologue. Further research clearly needs to be done to explore a number of outstanding issues: For example, we do not know yet about the hemispheric profiles in children younger than those tested here, and it will be of much interest to map the hemispheric profiles of individuals who are left-handed. Additionally, investigating the relationship between the intrinsic properties of the two hemispheres, such as spatial frequency or even categorical/coordinate abilities, which could ultimately give rise to these specializations, would be useful.

At the most general level, the data presented here support the idea that word selectivity in the left hemisphere and face selectivity in the right hemisphere do not develop independently. Despite being so intuitively different, when considering the similar computational constraints shared by words and faces, an interactive account for their developed specialization becomes far more plausible. This exploration into the development of hemispheric specialization for both words and faces reveals that the mechanisms giving rise to these adult patterns of lateralization are not as independent as commonly thought and that increasing literacy is the key pressure that triggers the emergence of bilateral hemispheric specialization.

References

Allison, T., Puce, A., Spencer, D. D., & McCarthy, G. (1999). Electrophysiological studies of human face perception. I: Potentials generated in occipitotemporal cortex by face and non-face stimuli. *Cerebral Cortex, 9,* 415–430. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/10450888. doi:10.1093/cercor/9.5.415

Aylward, E. H., Park, J. E., Field, K. M., Parsons, A. C., Richards, T. L., Cramer, S. C., & Meltzoff, A. N. (2005). Brain activation during face perception: Evidence of a developmental change. *Journal of Cognitive Neuroscience, 17,* 308–319. doi:10.1162/0898929053124884

Baker, C. I., Liu, J., Wald, L. L., Kwong, K. K., Benner, T., & Kanwisher, N. (2007). Visual word processing and experiential origins of functional selectivity in human extrastriate cortex. *Proceedings of the National Academy of Sciences of the United States of America, 104,* 9087–9092. doi:10.1073/pnas.0703300104

Cantlon, J. F., Pinel, P., Dehaene, S., & Pelphrey, K. A. (2011). Cortical representations of symbols, objects, and faces are pruned back during early childhood. *Cerebral Cortex, 21,* 191–199. doi:10.1093/cercor/bhq078

Carey, S., & Diamond, R. (1980). Maturational determination of the developmental course of face coding. in D. Caplan (Ed.), *The biological bases of cognitive processes* (pp. 60–93). Cambridge, MA: MIT Press.

Cohen, L., & Dehaene, S. (2004). Specialization within the ventral stream: The case for the visual word form area. *NeuroImage, 22,* 466–476. doi:10.1016/j.neuroimage.2003.12.049

Cohen, L., Dehaene, S., Naccache, L., Lehéricy, S., Dehaene-Lambertz, G., Hénaff, M.-A, & Michel, F. (2000). The visual word form area: Spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. *Brain, 123,* 291–307. doi:10.1093/brain/123.2.291

Cohen Kadosh, K., Cohen Kadosh, R., Dick, F., & Johnson, M. H. (2010). Developmental changes in effective connectivity in the emerging core face network. *Cerebral Cortex, 21,* 1389–1394. doi:10.1093/cercor/bhq215

Dehaene, S., & Cohen, L. (2011). The unique role of the visual word form area in reading. *Trends in Cognitive Sciences, 15,* 254–262. doi:10.1016/j.tics.2011.04.003

Dehaene, S., Pegado, F., Braga, L. W., Ventura, P., Nunes Filho, G., Jobert, A., . . . Cohen, L. (2010, December 3). How learning to read changes the cortical networks for vision and language. *Science, 330,* 1359–1364. doi:10.1126/science.1194140

de Heering, A., Turati, C., Rossion, B., Bulf, H., Goffaux, V., & Simion, F. (2008). Newborns' face recognition is based on spatial frequencies below 0.5 cycles per degree. *Cognition, 106,* 444–454. doi:10.1016/j.cognition.2006.12.012

de Schonen, S. D., Mancini, J., Camps, R., Maes, E., & Laurent, A. (2005). Early brain lesions and face-processing development. *Developmental Psychobiology, 46,* 184–208. doi:10.1002/dev.20054

de Schonen, S. D., & Mathivet, E. (1990). Hemispheric asymmetry in a face discrimination task in infants. *Child Development, 61,* 1192–1205. doi:10.1111/j.1467-8624.1990.tb02853.x

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,* 911–922.

Diamond, R., & Carey, S. (1977). Developmental changes in the representation of faces. *Journal of Experimental Child Psychology, 23,* 1–22. doi:10.1016/0022-0965(77)90069-8

Diamond, R., Carey, S., & Back, K. J. (1983). Genetic influences on the development of spatial skills during early adolescence. *Cognition, 13,* 167–185. doi:10.1016/0010-0277(83)90021-5

Ellis, H., Shepherd, J., & Bruce, A. (1973). The effects of age and sex upon adolescents' recognition of faces. *Journal of Genetic Psychology, 123,* 173–174.

Farah, M. J. (2000). *The cognitive neuroscience of vision*. Malden, MA: Blackwell.

Flin, R. H. (1985). Development of face recognition: An encoding switch? *British Journal of Psychology, 76,* 123–134. doi:10.1111/j.2044-8295.1985.tb01936.x

Gathers, A. D., Bhatt, R. S., Corbly, C., Farley, A., & Joseph, J. E. (2004, July). Developmental shifts in cortical loci for face and object recognition. *NeuroReport, 15,* 1549–1553. doi:10.1097/01.wnr.0000133299.84901.86

Germine, L. T., Duchaine, B., & Nakayama, K. (2011). Where cognitive development and aging meet: Face learning ability peaks after age 30. *Cognition, 118,* 201–210. doi:10.1016/j.cognition.2010.11.002

Golarai, G., Ghahremani, D. G., Whitfield-Gabrieli, S., Reiss, A., Eberhardt, J. L., Gabrieli, J. D. E., & Grill-Spector, K. (2007). Differential development of high-level visual cortex correlates with category-specific recognition memory. *Nature Neuroscience, 10,* 512–522. doi:10.1038/nn1865

Grüsser, O. J., & Landis, T. (1991). The splitting of “I” and “me”: Heautoscopy and related phenomena. In O. J. Grüsser & T. Landis (Eds.) & J. R. Cronly Dillon (Gen. Ed.), *Visual agnosias and other disturbances of visual perception and cognition* (pp. 297–303). Amsterdam, the Netherlands: MacMillian.

Guo, K., Meints, K., Hall, C., Hall, S., & Mills, D. (2009). Left gaze bias in humans, rhesus monkeys and domestic dogs. *Animal Cognition, 12,* 409–418. doi:10.1007/s10071-008-0199-3

Hasson, U., Levy, I., Behrmann, M., Hendler, T., & Malach, R. (2002). Eccentricity bias as an organizing principle for human high-order object areas. *Neuron, 34,* 479–490.

Hellige, J. B., Laeng, B., & Michimata, C. (2010). Processing asymmetries in the visual system. In R. Hugdahl & K. Westerhausen (Eds.), *The two halves of the brain: Information processing in the cerebral hemispheres* (pp. 379–415). Cambridge, MA: MIT Press.

Iaccino, J. F. (1993). *Left brain-right brain differences: Inquires, evidence, and new approaches*. Hillsdale, NJ: Erlbaum.

Joseph, J. E., Gathers, A. D., & Bhatt, R. S. (2011). Progressive and regressive developmental changes in neural substrates for face processing: Testing specific predictions of the Interactive Specialization account. *Developmental Science, 14,* 227–241. doi:10.1111/j.1467-7687.2010.00963.x

Kanwisher, N. (2000). Domain specificity in face perception. *Nature Neuroscience, 3,* 759–763. doi:10.1038/77664

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *NeuroImage, 17,* 4302–4311.

Kherif, F., Josse, G., & Price, C. J. (2011). Automatic top-down processing explains common left occipito-temporal responses to visual words and objects. *Cerebral Cortex, 21,* 103–114. doi:10.1093/cercor/bhq063

Kosslyn, S. M., Koenig, O., Barrett, A., Cave, C. B., Tang, J., & Gabrielli, J. (1989). Evidence of two types of spatial representations: Hemispheric specialization for categorical and coordinate relations. *Journal of Experimental Psychology: Human Perception and Performance, 15,* 723–735.

Le Grand, R., Mondloch, C. J., Maurer, D., & Brent, H. P. (2003). Expert face processing requires visual input to the right hemisphere during infancy. *Nature Neuroscience, 6,* 1108–1112. doi:10.1038/nn1121

Levy, I., Hasson, U., Avidan, G., Hendler, T., & Malach, R. (2001). Center-periphery organization of human object areas. *Nature Neuroscience, 4,* 533–539. doi:10.1038/87490

Marcel, T., Katz, L., & Smith, M. (1974). Laterality and reading proficiency. *Neuropsychologia, 12,* 131–139. doi:10.1016/0028-3932(74)90034-7

Maurer, U., Brandeis, D., & McCandliss, B. D. (2005). Fast, visual specialization for reading in English revealed by the topography of the N170 ERP response. *Behavioral and Brain Functions, 1,* 1–13. doi:10.1186/1744-9081-1-13

Maurer, U., Brem, S., Bucher, K., & Brandeis, D. (2005). Emerging neurophysiological specialization for letter strings. *Journal of Cognitive Neuroscience, 17,* 1532–1552. doi:10.1162/089892905774597218

Maurer, U., Rossion, B., & McCandliss, B. D. (2008). Category specificity in early perception: Face and word N170 responses differ in both lateralization and habituation properties. *Frontiers in Human Neuroscience, 2,* 1–7. doi:10.3389/neuro.09.018.2008

Mercure, E., Cohen Kadosh, K., & Johnson, M. H. (2011). The N170 shows differential repetition effects for faces, objects, and orthographic stimuli. *Frontiers in Human Neuroscience, 5,* 1–10. doi:10.3389/fnhum.2011.00006

Mondloch, C. J., Dobson, K. S., Parsons, J., & Maurer, D. (2004). Why 8-year-olds cannot tell the difference between Steve Martin and Paul Newman: Factors contributing to the slow development of sensitivity to the spacing of facial features. *Journal of Experimental Child Psychology, 89,* 159–181. doi:10.1016/S0022-0965(04)00108-0

Mondloch, C. J., Robbins, R., & Maurer, D. (2010). Discrimination of facial features by adults, 10-year-olds, and cataract-reversal patients. *Perception, 39,* 184–194. doi:10.1068/p6153

O’Hearn, K., Schroer, E., Minshew, N., & Luna, B. (2010). Lack of developmental improvement on a face memory task during adolescence in autism. *Neuropsychologia, 48,* 3955–3960. doi:10.1016/j.neuropsychologia.2010.08.024

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia, 9,* 97–113.

Passarotti, A. M., Paul, B. M., Bussiere, J. R., Buxton, R. B., Wong, E. C., & Stiles, J. (2003). The development of face and location processing: An fMRI study. *Developmental Science, 6,* 100–117. doi:10.1111/1467-7687.00259

Passarotti, A. M., Smith, J., DeLano, M., & Huang, J. (2007). Developmental differences in the neural bases of the face inversion effect show progressive tuning of face-selective regions to the upright orientation. *NeuroImage, 3,* 1708–1722. doi:10.1016/j.neuroimage.2006.07.045

Patterson, M. L., & Werker, J. F. (2002). Infants’ ability to match dynamic phonetic and gender information in the face and voice. *Journal of Experimental Child Psychology, 81,* 93–115. doi:10.1006/jecp.2001.2644

Peelen, M. V., Glaser, B., Vuilleumier, P., & Eliez, S. (2009). Differential development of selectivity for faces and bodies in the fusiform gyrus. *Developmental Science, 12*(6), F16–25. doi:10.1111/j.1467-7687.2009.00916.x

Phippard, D. (1977). Hemifield differences in visual perception in deaf and hearing subjects. *Neuropsychologia, 15,* 555–561. doi:10.1016/0028-3932(77)90059-8

Plaut, D. C., & Behrmann, M. (2011). Complementary neural representations for faces and words: A computational exploration. *Cognitive Neuropsychology, 28,* 251–275. doi:10.1080/02643294.2011.609812

Posner, M. I., & McCandliss, B. D. (1999). Brain circuitry during reading. In P. Klein & R. McMullen (Eds.), *Converging methods for understanding reading and dyslexia* (pp. 305–338). Cambridge, MA: MIT Press.

Price, C. J., & Devlin, J. T. (2011). The interactive account of ventral occipitotemporal contributions to reading. *Trends in Cognitive Sciences, 15,* 246–253. doi:10.1016/j.tics.2011.04.001

Puce, A., Allison, T., Asgari, M., Gore, J. C., & McCarthy, G. (1996). Differential sensitivity of human visual cortex to faces, letterstrings, and textures: A functional magnetic resonance imaging study. *The Journal of Neuroscience, 16,* 5205–5215. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/8756449

Robertson, L. C., & Ivry, R. (2000). Hemispheric asymmetries: Attention to visual and auditory primitives. *Current Directions in Psychological Science, 9,* 59–63. doi:10.1111/1467-8721.00061

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,* 1609–1624. doi:10.1016/j.neuroimage.2003.07.010

Scherf, K. S., Behrmann, M., & Dahl, R. E. (2012). Facing changes and changing faces in adolescence: A new model for investigating adolescent-specific interactions between pubertal, brain and behavioral development. *Developmental Cognitive Neuroscience, 2,* 199–219. doi:10.1016/j.dcn.2011.07.016

Scherf, K. S., Behrmann, M., Humphreys, K., & Luna, B. (2007). Visual category-selectivity for faces, places and objects emerges along different developmental trajectories. *Developmental Science, 10,* F15–F30. doi:10.1111/j.1467-7687.2007.00595.x

Schlaggar, B. L., Brown, T. T., Lugar, H. M., Visscher, K. M., Miezin, F. M., & Petersen, S. E. (2002, May 24). Functional neuroanatomical differences between adults and school-age children in the processing of single words. *Science, 296,* 1476–1479. doi:10.1126/science.1069464

Schlaggar, B. L., & McCandliss, B. D. (2007). Development of neural systems for reading. *Annual Review of Neuroscience, 30,* 475–503. doi:10.1146/annurev.neuro.28.061604.135645

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,* 14745–14753. doi:10.1523/JNEUROSCI.2238-11.2011

Sergent, J., Ohta, S., & MacDonald, B. (1992). Functional neuroanatomy of face and object processing: A positron emission tomography study. *Brain, 115,* 15–36. doi:10.1093/brain/115.1.15

Sergent, J., & Signoret, J.-L., & Rolls, E. T. (1992). Functional and anatomical decomposition of face processing: Evidence from prosopagnosia and PET study of normal subjects [and discussion]. *Philosophical Transactions of the Royal Society of London: Series B, Biological Sciences, 335,* 55–62. doi:10.1098/rstb.1992.0007

Spiridon, M., Fischl, B., & Kanwisher, N. (2006). Location and spatial profile of category-specific regions in human extrastriate cortex. *Human Brain Mapping, 27,* 77–89. doi:10.1002/hbm.20169

Tarr, M. (2008). *Stimulus images courtesy of Michael J. Tarr, Center for the Neural Basis of Cognition*. Pittsburgh, PA: Carnegie Mellon University. Retrieved from http://www.tarrlab.org

Teunisse, J.-P., & de Gelder, B. (2003). Face processing in adolescents with autistic disorder: The inversion and composite effects. *rain & Cognition, 52,* 285–294. doi:10.1016/S0278-2626(03)00042-3

Toga, A. W., & Thompson, P. M. (2003). Mapping brain asymmetry. *Nature Reviews Neuroscience, 4,* 37–48. doi:10.1038/nrn1009

Turkeltaub, P. E., Flowers, D. L., Lyon, L. G., & Eden, G. F. (2008). Development of ventral stream representations for single letters. *Annals of the New York Academy of Sciences, 1145,* 13–29. doi:10.1196/annals.1416.026

Twomey, T., Kawabata Duncan, K. J., Price, C. J., & Devlin, J. T. (2011). Top-down modulation of ventral occipito-temporal responses during visual word recognition. *NeuroImage, 55,* 1242–1251. doi:10.1016/j.neuroimage.2011.01.001

Wong, A. C., Bukach, C. M., Yuen, C., Yang, L., Leung, S., & Greenspon, E. (2011). Holistic processing of words modulated by reading experience. *PloS One, 6,* e20753. doi:10.1371/journal.pone.0020753

Yovel, G., & Kanwisher, N. (2005). The neural basis of the behavioral face-inversion effect. *Current Biology, 15,* 2256–2262. doi:10.1016/j.cub.2005.10.072

Received December 11, 2011
Revision received June 6, 2012
Accepted June 15, 2012 ■