Neuropsychologia 61 (2014) 315–323

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

An ERP investigation of the co-development of hemispheric lateralization of face and word recognition

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ARTICLE INFO

Article history:
Received 14 July 2013
Received in revised form
3 April 2014
Accepted 13 May 2014
Available online 13 June 2014

Keywords:
Hemispheric specialization
Lateralization
Face processing
Word processing
Event-related potentials

ABSTRACT

The adult human brain would appear to have specialized and independent neural systems for the visual processing of words and faces. Extensive evidence has demonstrated greater selectivity for written words in the left over right hemisphere, and, conversely, greater selectivity for faces in the right over left hemisphere. This study examines the emergence of these complementary neural profiles, as well as the possible relationship between them. Using behavioral and neurophysiological measures, in adults, we observed the standard finding of greater accuracy and a larger N170 ERP component in the left over right hemisphere for words, and conversely, greater accuracy and a larger N170 in the right over the left hemisphere for faces. We also found that although children aged 7–12 years revealed the adult hemispheric pattern for words, they showed neither a behavioral nor a neural hemispheric superiority for faces. Of particular interest, the magnitude of their N170 for faces in the right hemisphere was related to that of the N170 for words in their left hemisphere. These findings suggest that the hemispheric organization of face recognition and of word recognition does not develop independently, and that word lateralization may precede and drive later face lateralization. A theoretical account for the findings, in which competition for visual representations unfolds over the course of development, is discussed.

1. Introduction

The adult human brain appears to have highly specialized and seemingly independent neural systems for the visual processing of words and faces. Extensive evidence has demonstrated that the processing network for visual word recognition shows greater selectivity in the left over the right hemisphere, and, conversely, the processing network for face recognition shows greater selectivity in the right over the left hemisphere (for some early examples, see, e.g., Cohen and Dehaene (2004) and Kanwisher, McDermott, and Chun (1997)). The key issue addressed by the current work concerns the developmental emergence of this mature profile of lateralization and the degree of independence of these complementary patterns of hemispheric lateralization. Behavioral and neurophysiological data are presented that support a theoretical view in which the emerging hemispheric category-selectivity for word and face recognition are tightly coupled and are not independent of each other.

1.1. Emergence of word specificity

The dominance of the left over the right hemisphere for visual word processing is well established in right-handed adults (Grüsser & Landis, 1991; Hellige, Laeng, & Michimata, 2010). This left hemisphere (LH) superiority for words has long been demonstrated in behavioral studies, with participants showing an advantage for identifying orthographic stimuli presented in the right visual field (RVF) over those presented in the left visual field (LVF). Consistent with this, neurophysiological studies using event-related potentials (ERPs) have observed a N170 component that is stronger in the LH than in the RH in response to visually presented words (Maurer, Rossion, & McCandliss, 2008; Mercure, Cohen Kadosh, & Johnson, 2011). Additionally, neuroimaging studies have identified a region of the inferior temporal cortex, the Visual Word Form Area (VWFA; Talairach coordinates: $x=-43$, $y=-54$, $z=-12$), that shows greater selectivity for words over other visual stimuli in the left than right hemisphere (Cohen et al. 2000; Puce, Allison, Asgari, Gore, & McCarthy, 1996; for review, see Price & Devlin, 2011).

This selectivity for orthographic over non-orthographic stimuli is not present in pre-literate children and becomes apparent only after reading instruction and practice (Maurer, Brandeis, & McCandliss, 2005; Maurer, Brem, Bucher, & Brandeis, 2005). The left lateralization

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http://dx.doi.org/10.1016/j.neuropsychologia.2014.05.006
0028-3932/

increases with reading ability (Marcel, Katz, & Smith, 1974; Shaywitz et al., 2002) and the N170 continues to strengthen through adolescence (Posner & McCandliss, 1999; Schlaggar et al., 2002). This experience-dependent neural signature can also be observed in adulthood as the increased selectivity for learned orthography is seen functionally in adults learning to read a second language (Baker et al., 2007) and structurally in adults learning to read a first language (Carreiras et al., 2009).

1.2. Emergence of face specificity

Unlike with written words, children have extensive experience with processing faces right from birth and, given the social importance of faces, one might expect that there would be substantial evolutionary pressure to acquire early competence in face perception. Surprisingly, then, face selectivity follows the same prolonged developmental trajectory as words. Neuroimaging studies have identified a region in right inferior temporal cortex of adults that shows greater activation to upright compared with other non-face objects. This region has been referred to as the "Fusiform Face Area" (FFA; Talairach coordinates: $x=40$, $y=-55$, $z=-10$), (Kanwisher, 2000; Kanwisher et al., 1997; Sergent & Signoret, 1992; Spiridon, Fischl, & Kanwisher, 2006). Consistent with this, neurophysiological studies using ERPs have observed a N170 component that is stronger in the RH than in the LH in response to visually presented faces (Scott & Nelson, 2006). In children, selective activation of the FFA for faces is three times smaller than that in adults (Golarai et al., 2007) and emerges slowly through childhood and adolescence (Cohen Kadosh, Cohen Kadosh, Dick, & Johnson, 2010; 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 versus shoes, Cantlon, Pinel, Dehaene, & Pelphrey, 2010), the laterality pattern is still far from adult-like in 5–8 year olds (Scherf et al., 2007) and is not stable until early adolescence (12–14 years; Aylward et al., 2005).

The prolonged development of the neural organization of face recognition is also reflected in the protracted emergence of behavioral skill. Adult levels of performance are not achieved by 10-year-olds when they 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).

1.3. Coupled emergence of word and face hemispheric lateralization

Despite the common expectation that the emergence of visual word recognition and face recognition should be independent and that selectivity (and lateralization) for faces should be evident earlier than that for words, one recent theory has argued that the emergence of RH specialization for faces is contingent on the prior lateralization of words in the LH (Plaut & Behrmann, 2011; Behrmann & Plaut, 2013). On this account, by virtue of the fact that both faces and words rely on fine-grained visual acuity, they compete for higher-level visual representation in the mid-fusiform region (Hasson, Levy, Behrmann, Hendler, & Malach, 2002). The middle fusiform gyrus is ideally situated to optimize such representations given that it occupies the anterior extrapolation of the fovea in extrastriate cortex. Because the visual representations of words are subject to a top-down pressure to communicate with language-related information (particularly phonology), these orthographic representations become partially (although not exclusively) left-lateralized (hence the left hemisphere advantage for word processing). Consequently, to minimize competition for representation in the same cortical space as words (which ensues because the image statistics of faces and words are so dissimilar), faces become more (albeit not exclusively) right-lateralized. This face/word competition theory is supported by the finding that adults with no formal education in reading have heightened left-hemisphere activation to faces compared to literate controls, and that formal instruction in reading subsequently decreases the left, and increases the right, fusiform activation to faces (Dehaene et al., 2010). Similarly, young children show decreasing responses to faces in the left fusiform (VWFA) with increasing letter knowledge (Cantlon et al., 2011).

Additionally, within individual children, words become lateralized before faces, and the degree of face selectivity within an individual is predicted by standardized reading scores after regressing out quantitative reasoning scores, age, and accuracy on a face discrimination task (Dundas, Plaut, & Behrmann, 2013). This pattern of earlier hemispheric specialization for words than for faces (and their association) was obtained by hemifield behavioral measures that required participants (children, young adolescents and adults) to match a word or face stimuli in either the LVF or RVF with a centrally presented word or face. The index of hemispheric superiority was obtained by comparing the accuracy for judging stimuli presented in the two fields. Although these half-field measures reveal hemispheric superiorities for word and face recognition, they provide only rather general evidence regarding the neural basis of the hemispheric effects.

1.4. The current investigation

To examine neurophysiological markers of developmentally emerging hemispheric specificity, we recorded continuous electroencephalogram (EEG) and compared event related potentials (ERPs) in a group of children and a group of adults while they performed same/different discriminations of words and of faces. In particular, we chose to focus on the N170 ERP component because in ventral occipitotemporal cortex it has been associated with learned category selectivity (Rossion, Curran, & Gauthier, 2002). To be able to explore the developmental changes in the ERP signals, we included children across abroad range of ages (from 7 to 12 years of age). This was done deliberately so as to provide us with sufficient variability and range of word recognition competence in order to permit a correlation analysis between ERP signals and behavioral performance.

We expected to replicate our previous finding of a LH advantage for words in both groups and a RH advantage for faces in adults but not in children. If the neural correlates of face recognition and word recognition reflect the same lateralization profile, then the lateralization of the N170 component over posterior electrodes should follow a similar developmental profile, with a greater N170 response for words over the LH in both groups and a greater N170 response for faces over the RH but just for adults. Moreover, if the emergence of face lateralization is contingent on word lateralization, then the emergence of the RH N170 specificity for faces should be predicted by the specificity of the LH N170 for words. For completeness, we also explored neurophysiological signatures of face and word selectivity at other visual ERP components, the P100 and N250; however, we expected the lateralized emergence to be specific to the N170 component because of its association with category specificity.

2. Materials and methods

2.1. Participants

All participants were monolingual native English speakers and right-handed as determined by their having an index of 80 or higher (out of 100) on the Edinburgh Handedness Inventory. In the adult group, there were 17 individuals (10 males,