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Developmental differences for word processing in the ventral stream

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ABSTRACT

The visual word form system (VWFS), located in the occipito-temporal cortex, is involved in orthographic processing of visually presented words (Cohen et al., 2002). Recent fMRI studies in children and adults have demonstrated a gradient of increasing word-selectivity along the posterior-to-anterior axis of this system (Vinckier et al., 2007), yet whether this pattern is modified by the increased reading experience afforded by age is still in question. In this study, we employed fMRI and an implicit word-processing task, and then used a region of interest analysis approach along the occipito-temporal cortex to test the prediction that the selectivity for words along the extent of the VWFS differs between older experienced and younger novice readers. Our results showed differences between children and adults during word processing in the anterior left occipito-temporal cortex, providing evidence of developmental refinement for word recognition along the VWFS.

1. Introduction

Two decades of *in vivo* brain imaging studies of reading have been able to significantly advance our understanding of the functional neuroanatomy of the components of the reading process in typical and atypical readers (for reviews, see: Price et al., 2003; Pugh et al., 2001; Sandak, EinarMencl, Frost, & Pugh, 2004; Schlaggar & McCandliss, 2007). Specifically, a dorsal–ventral schema has been derived for the left hemisphere under which the ventral region (occipito-temporal cortex) has been functionally assigned as the visual orthographic system, specialized for fast processing of visually presented word forms, and relying on familiarity of word representations (Baker et al., 2007; Cohen et al., 2002; Dehaene et al., 2004; Maurer et al., 2006; Petersen, Fox, Snyder, & Raichle, 1990; Salmelin, Service, Kiesila, Uutela, & Salonen, 1996; Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999). The dorsal aspects on the other hand, host phonological and semantic processing in a distributed manner: temporo-parietal cortex subserves phonological manipulations (phonological awareness), phonological decoding (linking orthography to phonology), as well as semantic processing, while inferior frontal regions are involved in these same processes, together with articulation (Fiez & Petersen, 1998; Jobard, Crivello, & Tzourio-Mazoyer, 2003; Mechelli, Gorno-Tempini, & Price, 2003; Poldrack et al., 1999).

How these regions change developmentally as a consequence of reading experience has been a topic of recent research interest. Though methodological and practical challenges exist in examining the developmental trajectory of neural changes that occur with reading acquisition, several studies have been able to shed some light on the issue through cross-sectional studies involving beginning readers and adults (see Schlaggar & McCandliss, 2007 for a review). Consistent with models of typical reading acquisition (Pugh et al., 2001), younger normal readers have been observed to rely primarily on left temporo-parietal (dorsal) regions during word processing, while left inferior frontal regions are not observed until readers reach adulthood (Booth et al., 2001; Brown et al., 2005; Gaillard et al., 2003; Schlaggar et al., 2002; Shaywitz et al., 2002; Shaywitz et al., 2004; Turkeltaub, Gareau, Flowers, Zeffiro, & Eden, 2003). What is less clear is whether there is a developmental course in those ventral stream regions involved in orthographic processing, especially the so called "visual word form area" (VWFA – Cohen & Dehaene, 2004; Cohen et al., 2000, 2002; McCandliss, Cohen, & Dehaene, 2003).

In adult readers the VWFA consistently exhibits activation during word processing tasks, and has been shown to demonstrate selectivity for print over other types of stimuli such as checkerboards (Cohen et al., 2002), with an invariance for non-essential properties of the visual input such as case, font, size and location (Dehaene et al., 2001; Dehaene et al., 2004). It is considered to exhibit sensitivity to orthographic familiarity at the whole-word level (Bruno, Zumberge, Manis, Lu, & Goldman, 2008; Kronbichler et al., 2004, 2007) and would therefore seem to be a good candidate for showing modulation during the prolonged stages of reading acquisition. Specifically, the dorsal–ventral model of reading acquisition (Pugh et al., 2001) predicts that early readers rely

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primarily on the dorsal system during word processing (utilizing phonological assembly), with progressive development of the ventral system being hypothesized to occur with greater reading experience (providing direct lexical access through orthographic processing). However, studies by Schlaggar and colleagues (Brown et al., 2005; Schlaggar et al., 2002) which observed age-related increases in the left inferior frontal region during a task requiring subjects to provide a verbal response to a single presented word, concurrently observed greater activation for children than adults in the left extrastriate cortex, with these regions seemingly becoming less engaged in the more experienced readers. A study by Turkeltaub et al. (2003), utilizing an implicit word processing task (i.e. detection of a tall character within a visually presented real word or false-font), made a similar observation, reporting disengagement of right hemisphere ventral extrastriate regions in concurrence with developmental increases in the left inferior frontal region.

It has been suggested that developmental changes in the occipito-temporal region may not have been captured in this work by not studying populations that are young enough to demonstrate developmental changes here (Turkeltaub et al., 2003). Another explanation however, might be that these studies, focusing on the entire brain, and/or being bound to very specific anatomical locations, failed to capture more fine-grained developmental changes that occur within smaller regions of the ventral stream. A recent longitudinal study by Ben-Shachar and colleagues utilized a region-of-interest approach to examine developmental changes in visual word processing within the left occipito-temporal cortex (Ben-Shachar, Dougherty, Deutsch, & Wandell, 2011). Specifically, using an implicit reading task, they presented their pediatric participants with real words at different levels of visibility, demonstrating age-related changes in sensitivity to words in the left occipito-temporal sulcus, an area of cortex close to the classical VWFA. Based on the volume of activation observed in this region when contrasting visible vs. less/non- visible conditions, they noted that sensitivity in this area increases between the ages of 7–9 years, decreases after the age of 13 years, and stabilizes to adult levels at the age of 15 years. Thus, this study provided valuable information about developmental changes occurring around the vicinity of the VWFA. However, maturational cortical changes may extend beyond these specific patches of cortex, potentially occurring systematically across a larger portion of the occipito-temporal region. For example, a notable observation is the discovery that within the ventral stream there exists a posterior-to-anterior gradient of word-selectivity (i.e. greater differential activation in anterior regions between words and symbol strings), and a move towards a terminology that describes the "visual word form system" (VWFS). This gradient of word-selectivity has been demonstrated in adults (Vinckier et al., 2007) as well as in adolescents and children (Brem et al., 2006; Brem et al., 2009; van der Mark et al. 2009), primarily using region of interest (ROI) analysis. This approach has also been used to examine potential developmental differences. Brem et al. (2009) utilized a region of interest analysis within the ventral stream to examine whether any differences in the nature of the VWFS gradient of word-selectivity would be observed in children when compared to adolescents and adults in a Swiss-German speaking population. Their study employed a multi-modal approach, using both event related potential (ERP) and functional magnetic resonance imaging (fMRI) to take advantage of these technologies' respective strengths (i.e. ERP being more sensitive to fast transient responses and fMRI being more sensitive to sustained responses). The ERP results from this study suggest the existence of a tuning of the VWFS in more experienced readers, with greater preference for word processing being narrowed to more anterior portions of the occipito-temporal cortex in adults relative to children. However, this developmental specialization of word-selective regions was not observed in the fMRI data, potentially due to sustained responses from top-down processes elicited by the task demands. Interestingly, this study reports a negative correlation between reading fluency and word-selective fMRI activity in posterior occipito-temporal regions, thereby at least suggesting less engagement of posterior regions in more experienced readers.

The present study revisits the question about the spatial pattern of brain activity in the left occipito-temporal cortex as a function of reading development. If progressive selectivity for words in the anterior ventral stream is demonstrated in children, yet differs from the adults based on strength or location of selectivity, it does not only provide informed theoretical models of how the adult pattern is established (Vinckier et al., 2007), but it also provides a normative baseline for children by which to understand developmental disorders such as dyslexia, where a gradient of print selectivity has been shown to be lacking (van der Mark et al., 2009). We employed the same implicit reading task reported in Turkeltaub et al. (2003) and took steps to optimize our study for the question at hand: data were acquired at a higher field strength (3T as opposed to 1.5T) and similar to the study of Brem et al. (2009), we used a region of interest (ROI) analysis (rather than whole brain analysis) which allowed us to focus on the nature of the gradient of word-selectivity in the VWFS, and to explore whether greater specialization might be observed in the anterior portions of this region in more mature readers. In addition to within- and between-group analyses, we also examined how activation within this region related to measures of reading ability.

2. Materials and methods

2.1. Participants

All subjects were monolingual, native speakers of English. No individuals reported a previous diagnosis of developmental disability, severe language or psychiatric disorder. Twenty-six subjects (15 adults, 11 children) were included in final analysis after 17 (10 children) were excluded based on excessive head motion and poor in-scanner performance as described below. All subjects underwent a battery of behavioral tests measuring IQ, reading ability and skills known to support reading (Wagner & Torgesen, 1987) in order to ensure performance was in the normal range for both groups, and that children and adults had comparable performance levels. Tests included the Wechsler Abbreviated Scale of Intelligence (WASI) verbal and performance tests (Wechsler, 1999) and the Woodcock-Johnson Tests of Achievement (WJ-III) Basic Reading cluster to evaluate real and pseudoword reading (Woodcock, McGrew, & Mather, 2001). The Lindamood-Bell Auditory Conceptualization test (LAC) was employed to measure phonemic awareness (Lindamood & Lindamood, 2004) and Rapid Automatized Naming (RAN) for naming fluency (Denckla & Cutting, 1999; Denckla & Rudel, 1976a; Denckla & Rudel, 1976b). Group performance data on these measures as well as demographic information for the final group of subjects is listed in Table 1. Prior to the experiments, written informed consent was obtained from all participants, as well as from a legal guardian for the children. All experimental procedures were approved by the Georgetown University Institutional Review Board.

2.2. fMRI acquisition and task

During fMRI data acquisition, subjects performed an implicit word processing task (Price, Wise, & Frackowiak, 1996; Turkeltaub et al., 2003; Turkeltaub et al., 2004) involving the detection of a tall character within a visually presented real word (*RW*). Subjects