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Age, sex, and verbal abilities affect location of linguistic connectivity in ventral visual pathway

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ABSTRACT

Previous studies have shown that the *strength* of connectivity between regions can vary depending upon the cognitive demands of a task. In this study, the *location* of task-dependent connectivity from the primary visual cortex (V1) was examined in 43 children (ages 9–15) performing visual tasks; connectivity maxima were identified for a visual task requiring a linguistic (orthographic) judgment. Age, sex, and verbal IQ interacted to affect maxima location. Increases in age and verbal IQ produced similar shifts in maxima location; in girls, connectivity maxima shifted primarily laterally within the left temporal lobe, whereas the shift was primarily posterior within occipital cortex among boys. A composite map across all subjects shows an expansion in the area of connectivity with age. Results show that the *location* of visual/linguistic connectivity varies systematically during development, suggesting that both sex differences and developmental changes in V1 connectivity are related to linguistic function.

1. Introduction

Reading requires the conversion of visual information about component shapes into a recognizable lexical form. Reading words engages the ventral stream of visual processing, particularly left hemisphere regions involved in the processing of orthographic information (Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999; Brem et al., 2006; see also reviews by (Bolger, Perfetti, & Schneider, 2005; Cohen & Dehaene, 2004; Dehaene et al., 2010; Jobard, Crivello, & Tzourio-Mazoyer, 2003), as well as superior temporal and inferior parietal regions involved in phonological processing (Booth et al., 2002, 2003b; Booth, Mehdiratta, Burman, & Bitan, 2008; Jobard et al., 2003; Turkeltaub & Coslett, 2010). Young beginning readers recognize words based upon holistic characteristics such as word shape, whereas older more advanced readers use a combination of whole-word recognition and detailed awareness of letter combinations and their phonological representations (Ehri, 1995, 2005; Ehri & McCormick, 1998). These different strategies for word recognition areas are likely subserved by differential regions of cortex, regions which are highly interactive during word recognition and whose functional activity is highly correlated with task performance in various brain areas (Booth et al., 2008; Horwitz, Rumsey, & Donohue, 1998). Moreover, this interactivity develops as a function of experience and skill in young readers (Landi, Perfetti, Bolger, Dunlap, & Foorman, 2006), as orthographic and phonological processing in cortex is tuned to reflect the changing knowledge of spelling-to-sound relationships (Bolger, Hornickel, Cone, Burman, & Booth, 2008; Cao et al., 2010; Cone, Burman, Bitan, Bolger, & Booth, 2008; Maurer et al., 2006; Spironelli & Angrilli, 2009). These developmental changes in reading and language abilities should thus be reflected in changes in task-specific connectivity.

Interaction between visual and lexical areas is critical for reading. Visual processing in the ventral occipitotemporal region develops specificity for lexical stimuli during the acquisition of reading (Maurer et al., 2006), but this lexical specificity is delayed or absent in dyslexic children (Maurer et al., 2007, 2010) and pre-readers with low letter knowledge (Maurer, Brem, Bucher, & Brandeis, 2005). With difficulty converting visual information into phonology, dyslexic subjects show reduced responsivity to words (Helenius, Tarkiainen, Cornelissen, Hansen, & Salmelin, 1999; Salmelin, KiesilÃ¤, Uutela, & Salonen, 1996), likely due to reduced connectivity between occipitotemporal visual regions and phonological areas (Horwitz et al., 1998; Ligges, Ungureanu, Ligges, Blanz, & Witte, 2010; Pugh et al., 2000; Quaglino et al., 2008; Simos, Breier, Fletcher, Bergman, & Papanicolaou, 2000; van der Mark et al., 2011). Top-down lexical connections also modify occipitotemporal responses (Briem et al., 2009; Dikker, Rabagliati,

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& Pylkkänen, 2009; Foxe & Simpson, 2002; Liu et al., 2011; Pernet, Celsis, & Démonet, 2005; Quaglino et al., 2008; Yoncheva, Zevin, Maurer, & McCandliss, 2010), and may be essential to the acquisition of lexical selectivity within the ventral visual pathway (Dehaene et al., 2010). Connectivity from V1 reflects visual processing; changes in V1 connectivity during lexical tasks indicates where visual processing is first modified by lexical processes (a visual/lexical interaction).

Such psychophysiological interactions (Das et al., 2005; Friston et al., 1997) should reflect perceptual changes as readers mature and use different visual cues for word identification. Developmental differences in the size of lexical units used for word identification may be reflected in the *location* of task-specific connectivity due to the organization of visually-responsive cortex. Within the ventral stream of visual processing, visual information about component shapes is conveyed from the primary visual cortex (V1) to anterior regions in a hierarchical fashion, progressively sensitive to larger orthographic units (Cohen & Dehaene, 2004; McCandliss, Cohen, & Dehaene, 2003). For example, specificity for letters, syllables and words is seen within this ventral stream, extending from extrastriate occipital regions into the fusiform gyrus and inferotemporal cortex (Cohen et al., 2002; Kronbichler et al., 2004, 2007; Pegado, Nakamura, Cohen, & Dehaene, 2010; Schurz et al., 2010), with selectivity for larger units appearing further anterior within this region (Cohen et al., 2004a, 2002; Dehaene et al., 2004; Tagamets, Novick, Chalmers, & Friedman, 2000; Tarkiainen, Cornelissen, & Salmelin, 2003; Vinckier et al., 2007). As children grow older and improve reading performance, linguistic connectivity may thus shift (or expand) from the temporal lobe into occipital cortex, reflecting an increased awareness of individual letter combinations. Alternatively, lateral temporal regions show stimulus specificity for smaller (or more centralized) objects than medial temporal regions (Hasson, Harel, Levy, & Malach, 2003; Lerner et al., 2003; Levy, Hasson, Avidan, Hendler, & Malach, 2001; see also Chao, Martin, & Haxby, 1999; Maguire, Frith, & Cipolotti, 2001a); thus, increased awareness of letter combinations as children become better readers with age might instead result in a lateral shift (or expansion) of lexical connectivity within the temporal lobe. Such a shift would be analogous (but opposite in direction) to the lateral-to-medial shift in fusiform face processing with age with improvements in recognizing global features (Chao et al., 1999).

To demonstrate lexical changes in V1 connectivity, individual variability in language abilities must be considered. Several measures are potentially relevant. For example, the word ID and word attack subtests of the WJ-III are standardized measures of the ability to read words and pseudowords, respectively; if differences in connectivity account directly for differences in reading ability at a given age (e.g., via bottom-up processes), shifts in connectivity should be correlated with either or both of these scores. On the other hand, posterior or lateral shifts in connectivity may instead reflect top-down processes that reflect more general verbal abilities and experiences relevant to reading skills. For example, vocabulary influences reading comprehension and exception word reading (Ricketts, Nation, & Bishop, 2007). The acquisition of new vocabulary is itself influenced by orthographic knowledge (Ehri & Rosenthal, 2007), suggesting that visual areas involved in processing orthography interact with language areas involved in vocabulary acquisition. Vocabulary and knowledge of word similarities are both incorporated into verbal IQ (an age-normalized measure of verbal language abilities), and verbal IQ is correlated with both structural (Ramsden et al., 2011) and functional variability in cortical language processing (Everts et al., 2009; Lidzba, Schwilling, Grodd, Krägeloh-Mann, & Wilke, 2011). Because it reflects verbal abilities and knowledge relevant to reading, higher verbal IQ could result in either the posterior or lateral shift in connectivity (as described above).

The sex of a subject is also likely to be relevant. Developmentally, girls are generally more advanced for language (Bornstein, Hahn, & Haynes, 2004; Han & Hoover, 1994; Lynn, 1992; Mann, Sasanuma, Sakuma, & Masaki, 1990; Martin & Hoover, 1987; Martins et al., 2005; Undheim & Nordvik, 1992). During orthographic and phonological tasks, girls and boys differ in the lateralization of evoked potentials (Spironelli, Penolazzi, & Angrilli, 2010); furthermore, girls' fMRI activation within the left fusiform gyrus is greater than boys and correlated with performance accuracy, even after accounting for age and language skill (Burman, Bitan, & Booth, 2008). Thus, one may hypothesize that the primary focus of connectivity in the visual ventral stream depends on age, verbal IQ, and the sex of a subject.

Considering these influences, we wondered whether there are individual differences in language-specific connectivity within the visual system that could be relevant to reading. More specifically, is the location of maximal language-specific connectivity from V1 affected by age, sex or verbal IQ? To identify the earliest visual area involved in language function, this study examines regions in the ventral stream of children whose connectivity with primary visual cortex (V1) increases when making orthographic comparisons between words. The left occipitotemporal response to words depends on language lateralization (Cai, Paulignan, Brysbaert, Ibarrola, & Nazir, 2010; Rossion, Joyce, Cottrell, & Tarr, 2003; Spironelli & Angrilli, 2007), with laterality of language function in occipitotemporal regions increasing with age (Everts et al., 2009; Spironelli & Angrilli, 2009); thus, developmental changes in connectivity associated with language function should occur preferentially in the left hemisphere. In the current study, psychophysiological interactions are used to identify the region whose connectivity with V1 is most strongly modulated by the linguistic component of an orthographic comparison task (i.e., the connectivity maximum); the effects of age, sex, verbal IQ, and standardized reading scores on the location of this maximum within the ventral stream of visual processing is then examined separately for the left and right hemispheres.

2. Methods

2.1. Subjects

Forty-two healthy children participated in the study (ages 9–15, mean 11.3, 20 females). Children were recruited from the Chicago metropolitan area; the Institutional Review Board at Northwestern University and Evanston Northwestern Healthcare Research Institute approved the informed consent procedures. Parents of children were given an interview to exclude participants having a previously reported history of intelligence, reading, attention, or oral-language deficits. All children were described as free of neurological diseases or psychiatric disorders and were not taking medication affecting the central nervous system. Children were native English speakers, with normal hearing and normal or corrected-to-normal vision. Included children were all right handed (mean = 78.2, range 50–90) according to the 9-item Likert scale questionnaire (−90 to 90, positive scores indicate right hand dominance).

Subjects fell into one of 4 age groups at the time of their testing (birthdays within 4 months of their specified age): age 9, 11, 13 or 15. Standardized intelligence test scores (Wechsler, 1999) showed an average full scale IQ of 116 (range of 94–146, SD = 12.6); Verbal IQ of 116.3 (range of 79–142, SD = 14.1); and performance IQ = 108.9 (range of 79–139, SD = 14.7). The verbal IQ component of this test includes subtests of Vocabulary and Similarities (verbal reasoning and concept formation). The average standardized reading score (Woodcock, Mather, McGrew, & Schrank, 2001) was 107.2 for nonword reading accuracy (range of 88–125, SD = 9.8)