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DEVELOPMENTAL FMRI STUDY: FACE AND OBJECT RECOGNITION

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ABSTRACT OF DISSERTATION

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DEVELOPMENTAL FMRI STUDY: FACE AND OBJECT RECOGNITION

ABSTRACT OF DISSERTATION

A dissertation submitted in partial fulfillment of the
requirements for the degree of Doctor of Philosophy in the
College of Medicine
at the University of Kentucky

By
Ann D. Gathers

Lexington, Kentucky

Co-Directors: Dr. Greg Gerhardt, Professor of Anatomy and Neurobiology
Dr. Jane Joseph, Assistant Professor of Anatomy and Neurobiology

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Visual processing, though seemingly automatic, is complex. Typical humans process objects and faces routinely. Yet, when a disease or disorder disrupts face and object recognition, the effects are profound. Because of its importance and complexity, visual processing has been the subject of many adult functional imaging studies. However, relatively little is known about the development of the neural organization and underlying cognitive mechanisms of face and object recognition. The current project used functional magnetic resonance imaging (fMRI) to identify maturational changes in the neural substrates of face and object recognition in 5-8 year olds, 9-11 year olds, and adults. A passive face and object viewing task revealed cortical shifts in the face-responsive loci of the ventral processing stream (VPS), an inferior occipito-temporal region known to function in higher visual processing. Older children and adults recruited more anterior regions of the ventral processing stream than younger children. To investigate the potential cognitive basis for these developmental changes, researchers implemented a shape-matching task with parametric variations of shape overlap, structural similarity (SS), in stimulus pairs. VPS regions sensitive to high SS emerged in older children and adults. Younger children recruited no structurally-sensitive regions in the VPS. Two right hemisphere VPS regions were sensitive to maturational changes in SS. A comparison of face-responsive regions from the passive viewing task and the VPS SS regions did not reveal overlap. Though SS drives organization of the VPS, it did not explain the cortical shifts in the neural substrates for face processing. In addition to VPS regions, results indicated additional maturational SS changes in frontal, parietal, and cerebellar regions. Based on these findings, further analyses were conducted to quantify and qualify maturational changes in face and object processing throughout the brain. Results indicated developmental changes in activation extent, signal magnitude, and lateralization of face and object recognition networks. Collectively, this project supports a developmental change in visual processing between 5-8 years and 9-11 years of age. Chapters Four through Six provide an in-depth discussion of the implications of these findings.

KEYWORDS: neuroimaging, visual processing, development, ventral processing stream, structural similarity processing

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June 29, 2005

DEVELOPMENTAL FMRI STUDY: FACE AND OBJECT RECOGNITION

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RULES FOR THE USE OF DISSERTATIONS

NAME	DATE

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In memory of

my grandmother, Agnes Harbison
and my uncle, Ron Harbison

For beginning this journey with me
and believing that I would see it to completion.

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In the entrance of Boston's Old City Hall are written the words of Benjamin Franklin "An investment in knowledge pays the best interest". The pursuit of my doctoral degree has certainly been an investment– an investment of time measured in long days, late nights, and weekends culminating in years and an investment of resources measured in mental and emotional energy and strain. The costs of this pursuit were well-thought through five years ago. The decision to leave an established career and to return to school to pursue another degree was, like all calculated risks and heart-held visions, an initial sacrifice with promises of potential fulfillment and great reward. In the end, the gentle guiding words of my grandmother, Agnes Harbison, encouraged me to take the risk and make the investment.

Every good investment produces interest. The pursuit of my Ph.D. has most certainly been an investment in knowledge with great interest. My degree is in the sciences and as a result I have gained much in the way of understanding cells and systems, identifying structures and functions, collecting and analyzing data, and applying and interpreting results. My knowledge of my field has grown immensely. However, the graduate school experience should not be limited to gaining expert knowledge in one's own field. My graduate education goes beyond neuroscience. I have had opportunities to learn sociology through both personal and professional relationships, geography and culture through international friendships and travels (from Veracruz to Budapest), and kinesiology from rock climbing, running the Bluegrass 10,000, and bike trekking to Shakertown. From formal and informal educational experiences during graduate school, I have learned to apply effort, accept challenges, manage time, and value differences. In all of this, my grandmother was right. The time would pass quickly and the end would be worth the effort.

Benjamin Franklin mentioned the interest gained from an investment in knowledge but he failed to mention the debt. I have certainly gained a large amount of intangible interest; however, I could not have accomplished this alone. I owe a great debt of thanks to many who have contributed to the successful completion of my degree and the achievement of a dream. To my mentor, Dr. Jane E. Joseph, I owe many thanks for my training in research skills and for opportunities and encouragement to present at international conferences. To my committee members, Dr. Ramesh Bhatt, Dr. Wayne Cass, and Dr. Greg Gerhardt, I offer deep appreciation for their continual guidance and support throughout the course of my doctoral education. To the Joseph Lab crew, past and present, you have been a wonderful team with which to work and play. To Agnes Bognar, Robin Avison, and Indrias Behrane, I offer appreciation for technical support. To the Anatomy and Neurobiology Department faculty and staff, I owe thanks for advice and guidance, opportunities to teach, many answered questions about funding and reimbursement, paid health fees, scheduled meeting rooms, and fresh brewed coffee. And of course, to the volunteers and their families who participated in this research, I owe my deepest gratitude for their time, patience, and cooperation.

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I. Introduction

Facing a Life without Recognition

During the average human life span, we are exposed to and are required to process a myriad of faces and objects. As a result, lack of competent face and object recognition skills may hamper functioning in society. Seizures, meningitis, traumatic brain injuries, ischemia, heredity, and degenerative diseases can produce visual processing deficits in adults and children such as difficulties in object recognition (visual agnosia) (Farah, 1990; Moore & Price, 1999; Moscovitch, Winocur, & Behrmann, 1997b) and/or face recognition (prosopagnosia) (Bentin, Deouell, & Soroker, 1999b; Stiers & al., 2001; Stiers, De Cock, & Vandenbussche, 1999). For some developmental prosopagnosias there is no known etiology (Bentin, Deouell et al., 1999b; de Gelder & Rouw, 2000a). Whether acquired or congenital, agnosias can hinder activities of daily living and social interactions (Barton, Cherkasova, Press, Intriligator, & O'Connor, 2003; Duchaine & Nakayama, 2005; Humphreys & Riddoch, 2003; Kress & Daum, 2003).

Prosopagnosia is rare but studies show that similar perceptual deficits and adverse social affects may occur in a more well-known group of disorders, autism spectrum disorders (ASD). Though individuals with an ASD present with a wide range of characteristics and levels of severity (Folstein & Rosen-Sheidley, 2001) (see review Eigsti & Shapiro, 2003); lack of interest and attention to the human face are hallmark symptoms (Cohen & Volkmar, 1997). Aversion to the human face and related social impairments in individuals with an ASD may be founded on the use of aberrant perceptual strategies for object and face processing (Hubl et al., 2003; Lopez, Donnelly, Hadwin, & Leekam, 2004; Mottron & Belleville, 1993). Atypical perceptual strategies in ASD occur at many levels of face processing. For instance, a mark of normal perceptual differences in face and object processing is the face inversion effect. The inversion effect refers to the finding that typical adults perform more poorly on inverted faces than on upright faces and upright and inverted non-face stimuli in recognition tasks. This disproportionate interference suggests a disruption of relational processing strategies (e.g. distance between eyes) and an increased reliance on facial features or parts for recognition (Bartlett & Searcy, 1993; Carey & Diamond, 1994; Tanaka & Farah, 1993, 2003). In ASD children, face recognition performance is less affected by inversion than in non-autistic peers

(Hobson, Ouston, & Lee, 1988; Tantam, Monagham, & Nicholson, 1989). The absence of a strong face inversion effect in ASD subjects supports a featural bias for face perception. This featural bias in ASD individuals extends to non-face stimuli as evidenced by their superior perception of object parts (Jolliffe & Baron-Cohen, 1997; Shah & Frith, 1983). A featural bias in individuals with an ASD indicates atypical rather than absent relational processing (Hubl et al., 2003; Joseph & Tanaka, 2003; Lopez et al., 2004; Teunisse & de Gelder, 2003). Atypical relational processing has been attributed to abnormal visual search strategies (Hubl et al., 2003; Teunisse & de Gelder, 2003), attention shifting difficulties (Casey, Winner, Benbow, Hayes, & DaSilva, 1993; Courchesne, Townsend, Akshoomoff, Saitoh, & al., 1994), and uncharacteristic selective attention to face parts (i.e. a preference for the mouth as opposed to the eyes) (Joseph & Tanaka, 2003). The perceptual dysfunctions found in ASD extend beyond the general identification problems in prosopagnosics to a range of pragmatic impairments including difficulties interpreting facial expressions and using contextual information for appropriate social responses (Hadjikhani et al., 2004; Ozonoff, Pennington, & Rogers, 1990; Teunisse & de Gelder, 2003). Some neuroimaging studies suggest that structural and functional brain abnormalities are the basis of the socially crippling perceptual deficits characteristic of ASD (Critchley, Daly, Phillips et al., 2000; Pierce, Haist, Sedaghat, & Courchesne, 2004; Pierce, Muller, Ambrose, Allen, & Courchesne, 2001; Schultz et al., 2000) (see review Boddaret & Zilbovicius, 2002; Rumsey & Ernst, 2000) though not all data support this idea (Volkmar & al., 1989). Collectively, however, research on autism and related disorders supports abnormal perceptual processing (Hobson et al., 1988; Hubl et al., 2003; Joseph & Tanaka, 2003; Lopez et al., 2004; Tantam et al., 1989) the nature and neural substrates of which need further clarification. Hence, evidence of disruptions in the day-to-day lives of children and adults suffering with agnosias and ASD motivate the need to study the perceptual processes and corresponding neural correlates of face and object recognition.

Visual Processing and The Ventral Processing Stream

Because of their impact on our daily lives, face and object processing have been studied for decades. To thoroughly investigate the visual processing of faces and objects, scientists use a variety of behavioral, neuroimaging, and electrophysiological techniques. The ventral processing stream (VPS) is at the core of these investigations. The VPS is a functional brain region involved in visual recognition (Damasio, Damasio, & Van Hoesen, 1982; Desimone, Schein, Moran, & Ungerleider, 1985; Gauthier, Skudlarski, Gore, & Andersen, 2000; Goodale & Milner, 1992; Gorno-Tempini & Price, 2001; Haxby et al., 1999; Joseph & Gathers, 2003; Kanwisher, McDermott, & Chun, 1997; Malach et al., 1995; Milner & Goodale, 1995). It consists anatomically of the lingual, fusiform, and inferior temporal gyri. Neurons in the VPS are specialized for processing object features including shape, color, texture, and orientation (Desimone et al., 1985; Komatsu & Ideura, 1993; Livingstone & Hubel, 1988). Though the general anatomical boundaries and cellular components are known, the functional organization and corresponding cognitive mechanisms of the VPS are not yet fully understood. A review of the literature reveals three unresolved questions regarding the VPS and visual processing:

1.) What is the functional architecture of the VPS in regards to visual processing?
2.) What principle cognitive mechanism(s) shape VPS functional architecture?
3.) What is the course of functional development in the VPS?

The present work was designed to investigate these questions. Here pertinent theories and findings in literature will be discussed followed by an explanation of the focus and methods of this project as they relate to the continuing controversies regarding the cognitive and neural bases of face and object processing.

II. Background

<u>1.) What is the functional architecture of the VPS?</u>

From lesion studies and brain imaging studies of healthy adults, two main hypotheses emerge concerning the functional organization of the VPS. First, some studies suggest that the VPS is organized into groups of neurons (modules) that function in the recognition of specific categories (Downing, Jiang, Shulman, & Kanwisher, 2001; Duchaine, 2000; Duchaine & Nakayama, 2005; Kanwisher et al., 1997; Kanwisher, Stanley, & Harris, 1999; Kendrick, da Costa, Leigh, Hinton, & Peirce, 2001; O'Craven & Kanwisher, 2000; Spitzer, Kwong, Kennedy, Rosen, & Belliveau, 1995). For example, neuroimaging studies have identified a cortical area dedicated to face processing (Fusiform Face Area) (Kanwisher et al., 1997), another to body parts (Extrastriate Body Area) (Downing et al., 2001), another to scenes (Parahippocampal Place Area) (Epstein, Harris, Stanley, & Kanwisher, 1999), another to letters (Gros, Boulanouar, Viallard, Cassol, & Celsis, 2001; Polk & Farah, 1998), and yet another to word forms (Leff et al., 2001; Petersen, Fox, Snyder, & Raichel, 1990). The idea of dedicated brain modules is termed domain-specific organization. Second, other studies posit distributed patterns of brain activation in the VPS with overlapping neural substrates among categories, implying a domain-general organization (Gauthier, Behrmann, & Tarr, 1999; Haxby et al., 2001; Joseph, Partin, & Jones, 2002). Support for both of these views is discussed here.

Domain-Specific Organization

Prosopagnosia

Neuropsychological, neuroimaging, and electrophysiological studies of patients suffering from categorical recognition impairments constitute much of the evidence for domain-specific functional organization of the brain. A number of prosopagnosia cases claim dissociations between impaired face recognition and intact to relatively intact non-face recognition (Barton et al., 2003; Barton, Press, Keenan, & O'Conner, 2002; Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999; de Gelder, Bachoud-Levi, & Degos, 1998; de Gelder & Rouw, 2000a; Duchaine, 2000; Duchaine & Nakayama, 2005; Farah, Levinson, & Klein, 1995; Farah, Rabinowitz, Quinn, & Liu, 2000; Farah, Wilson, Drain, & Tanaka, 1995; Hasson, Avidan, Deouell, Bentin, & Malach, 2003; Kress & Daum, 2003; Marotta, Genovese, & Behrmann, 2001; McNeil & Warrington, 1993; Rossion et al., 2003). A minority of child and adult-onset prosopagnosias are limited to face perception deficits (Bentin, Deouell, & Soroker, 1999a; Bentin, Deouell et al., 1999b; Bentin, Mouchetant-Rostaing et al., 1999; de Gelder & Rouw, 2000a; Duchaine, 2000; Duchaine & Nakayama, 2005; Kress & Daum, 2003). Neuropsychological testing reveals that many prosopagnosic subjects are impaired in other areas of cognition including visuo-spatial skills (Barton et al., 2003; Duchaine, 2000), central auditory processing (Duchaine, 2000); reading (Ariel & Sadeh, 1996; Barton, Zhao, & Keenan, 2003; Rossion et al., 2003); and verbal and non-verbal memory (Barton et al., 2003; Barton et al., 2002). However, recognition deficits in prosopagnosics are primarily face-specific with essentially normal performance on low-level vision and general object recognition tasks (de Gelder et al., 1998; de Gelder & Rouw, 2000a; Duchaine, 2000; Hasson et al., 2003; Kress & Daum, 2003; Marotta et al., 2001; Rossion et al., 2003) (c.f. Ariel & Sadeh, 1996; Barton et al., 2003; Barton et al., 2002; Campbell, 1992; McNeil & Warrington, 1993; Young & Ellis, 1989).

Findings from functional magnetic resonance imaging (fMRI) investigations of prosopagnosia support face-specific abnormal VPS activation patterns in patients relative to control subjects (Hadjikhani & de Gelder, 2002; Marotta et al., 2001; Rossion et al., 2003) (c.f. Hasson et al., 2003). Prosopagnosic patterns differ from normal patterns in two primary aspects. Unlike controls, prosopagnosics fail to produce significantly greater activation for faces than other non-face stimuli. In addition, face stimuli fail to significantly activate face-responsive fusiform regions (e.g. Kanwisher, 1997) identified in controls (Hadjikhani & de Gelder, 2002; Marotta et al., 2001).

Similarly, event-related potentials (ERPs) in prosopagnosics provide evidence for domain-specificity. Whereas fMRI data provide the location of neural activity, ERP's reflect the timing of neural functions. In individuals with normal functioning perceptual processes, a negative going component in the human electroencephalogram termed the 'N170' is specifically amplified for faces compared to other stimuli (Eimer, 1998, 2000). In contrast, the differential activation of the N170 between face and non-face stimuli is reduced or absent in congenital and adult-onset prosopagnosia patients (Eimer & McCarthy, 1999; Kress & Daum, 2003). In other words, the lack of a face-specific N170 response in individuals with face processing deficits indicates that typical face processing, in contrast to non-face object processing, relies upon more specific neural activity.

Though these investigations offer some support for functionally selective domains, data from pure cases of prosopagnosia (Bentin, Deouell et al., 1999a; Duchaine, 2000; Duchaine & Nakayama, 2005; Kress & Daum, 2003; Rossion et al., 2003), in which no other recognition deficits exist, provide the strongest argument for domain specificity (Gauthier, Behrmann et al., 1999). The existence of a face processing deficit in the absence of any non-face recognition deficits, and vice versa, would indicate that face processing is specialized and may rely on unique neural substrates. Such a double dissociation of face-specific and non-face specific recognition deficits would serve as evidence for domain-specific neural substrates. However, considering all the interconnections of the brain, pure cognitive deficits of any kind are rare. Prosopagnosia is no exception. In a behavioral study comparing face processing with six other object categories, Duchaine and Nakayama tested seven prosopagnosia patients presenting with intact object recognition skills (2005). Though considerable heterogeneity existed, reaction times and performance measurements for all subjects indicated differential processing of faces from all other stimulus classes tested. Pure face recognition deficits in these subjects imply a reliance on separate cognitive processes for faces and objects. Though Duchaine & Nakayama's behavioral findings make a strong case for differential processing of objects and faces, evidence of cortical dissociation is also needed to argue a domain-specific VPS organization.

Using fMRI tasks to ascertain neural correlates of face and object recognition in a pure prosopagnosic, Rossion and colleagues provide support for face-specific processing regions (2003). Extensive neuropsychological testing of their subject, patient P.S., revealed deficits in face but not object recognition and naming. In a one-back fMRI task, control subjects and P.S. were required to detect repetitions of faces and within-class non-face object stimuli. All subjects produced significantly greater activation for objects than faces in bilateral parahippocampal regions. Also, as in controls, the right middle fusiform gyrus of P.S. was significantly activated for the comparison of faces versus objects. Other neuroimaging data in normal individuals verify activation of the right mid-fusiform gyrus for face stimuli relative to non-face stimuli (Kanwisher et al., 1997). In addition to the right mid-fusiform area, a significant face versus objects response occurred in the right inferior occipital gyrus (IOG) of normal subjects, a damaged area in P.S.'s brain. Thus, control subject data revealed a well-localized bilateral object recognition system in the parahippocampal gyrus distinct from face recognition substrates in the right mid-fusiform and inferior occipital gyri. Furthermore, impaired face recognition and a lesioned, non-functional IOG in P.S. in conjunction with strong faces versus objects signals in the IOG of controls indicated a specific sufficient and necessary face processing region.

Behavioral testing of pure prosopagnosics suggests face and object recognition involve different cognitive mechanisms. Imaging data from a prosopagnosia study testifies to separate neural correlates for face and object recognition. Together, these findings signify that face recognition is specialized and, potentially, localized to a specific cortical region. However, a comparable case of pure non-face recognition impairment must exist to verify a double dissociation of neural processes for face and object recognition.

Other Disorders

Clinical cases of spared non-face recognition and impaired face recognition contribute to the idea of domain-specific regions of the VPS. To further the argument regarding domain-specific modules, multiple reports exist of patients with problems recognizing and naming particular object categories. Reviews (see Capitani, Laiacona, Mahon, & Caramazza, 2003; Caramazza & Shelton, 1998; Forde & Humphreys, 1999; Humphreys & Forde, 2001; Tyler & Moss, 2001) provide a synopsis of evidence for recognition impairments at broad levels of categorization (i.e. living and non-living things). Individual cases within these broad groupings of more specific category impairments (i.e. deficits in fruit and vegetable recognition but not in animal recognition (Farah & Wallace, 1992), provide additional evidence for a modular VPS. However, as with prosopagnosia, category exclusive deficits, presenting the strongest argument for domain-specificity, are rare (Capitani et al., 2003). Such a case is that of CK. CK presented with severe object agnosia accompanied by dyslexia; however, he had no deficits in face processing. When processing numerous versions of face stimuli (i.e. cartoons, degraded and fractured), CK's performance on neuropsychological tests was comparable to that of normal subjects (Moscovitch, Winocur, & Behrmann, 1997a). Only when the task involved a face stimulus whose parts were made of objects did CK's performance vary significantly from that of the control. CK recognized the stimulus as a face but, unlike controls, he did not express a consistent awareness that the face was composed of objects. These results indicate a perceptual impairment in object but not face processing – a case of object-specific agnosia. Together, cases of face-specific and object-specific agnosia provide evidence of a double dissociation between face and object recognition implying two distinct processing systems. However, neuroimaging evidence of disparate face and object substrates in a case of non-face agnosia is needed to fully support a domain-specific VPS.

In addition to case studies of agnosia, three fMRI studies in autistics provide some basis for category-specific VPS functional organization. When individuals presenting with autism or an ASD viewed neutral faces (Pierce et al., 2001; Schultz et al., 2000) and emotional faces (Critchley, Daly, Phillips et al., 2000), abnormal patterns of activation relative to controls emerged in fusiform regions previously identified as the fusiform face area (FFA) (Kanwisher et al., 1997). Pierce and colleagues report a seemingly paradoxical find in their fMRI face versus shape perception task. Performance, as measured by reaction time and error rates, did not statistically differ between autistics and controls. In contrast, imaging data revealed reduced responses in the face-sensitive fusiform and inferior occipital regions in autistics relative to controls. Though performance measures indicate autistics process faces normally, their functional patterns support the use of aberrant perceptual strategies. In controls, face processing consistently recruited particular neural substrates, anterior fusiform regions, whereas, in autistics, face processing did not correspond to any consistent area of activation but rather was characterized by idiosyncratic brain activation patterns. Similarly, Schultz et al. report atypical neural correlates for face processing in high functioning individuals with an ASD (2000). One group of ASD subjects and two matched control groups participated in a fMRI face and subordinate level object perception task. The brain patterns of both normal groups revealed face versus object responses in the fusiform gyrus and object versus face responses in the inferior temporal gyrus (ITG). In contrast, the same inferior temporal region in ASD subjects was significantly activated by the face versus object condition. A between-groups analysis indicated control subjects produced greater fusiform activation for faces than the ASD group. Behavioral data provided inconclusive support for brain response patterns as only one of the two control groups performed significantly better on face discrimination than the ASD group. Though behavioral data from the Pierce et al., and Shultz et al., studies fail to shed light on the cognitive face processing mechanisms used by individuals with an ASD, they do provide data on the neural substrates of normal versus abnormal face processing. In this study, as in the aforementioned fMRI investigation, normal subjects consistently activate a fusiform region during face processing tasks. These same neural substrates for face processing are not evident in individuals with autism and related disorders.

In their study of emotional face perception in autistics, Critchley and colleagues provide behavioral and functional data that support atypical face processing in autistics and strengthen arguments for face-specific neural substrates in normal face processing (2000). Using neutral and emotional (i.e. happy, sad, angry) face stimuli in an fMRI task of explicit and implicit memory, the authors report significantly greater errors in autistic than normal controls on the explicit memory task. Poorer performance by autistics than their normal peers on an emotional face discrimination task corresponds with functional findings. Compared to the controls, autistics do not produce significant activation in the right fusiform gyrus during the emotions face memory task.   Again, face processing in normal controls consistently recruits similar regions in the fusiform gyrus whereas face processing in individuals with an ASD is atypical in its functional organization. Together, these studies of ASD indicate that a face-responsive neural substrate in the fusiform gyrus is involved in normal face processing.

Normal Healthy Adults

Though studies of lesions and disorders provide insight, alone, they can not provide a sufficient explanation of typical VPS organization. Because brain damaged patients may differ in performance or processing routes from normal subjects (de Gelder, Frissen, Barton, & Hadjikhani, 2003; de Gelder & Rouw, 2000b) and because brain damage generally has poor anatomical definition (Gorno-Tempini, Wenman, Price, Rudge, & Cipolotti, 2001), research must be conducted in healthy, normal subjects for an accurate assessment of normal functional organization. Fortunately, information in normal healthy adults abounds. A broad range of category divisions have been investigated using an equally broad range of techniques.

Functional imaging studies of healthy adults have identified category-specific neural correlates including but not limited to the following classifications: 1. non-living (Chao & Martin, 2000; Leube, Erb, Grodd, Bartels, & Kircher, 2001; Martin, Wiggs, Ungerleider, & Haxby, 1996) and 2. living things (including living things relative to tools) (Martin et al., 1996; Perani et al., 1999); 3. faces (Andrews & Schluppech, 2004; Gorno-Tempini & Price, 2001; Kanwisher et al., 1997; Kanwisher et al., 1999; Nakamura, Kawashima et al., 2000; Puce, Allison, Gore, & McCarthy, 1995; Sergent, Ohta, & MacDonald, 1992); 4. body parts (Downing et al., 2001); 5. places and scenes (Gorno-Tempini & Price, 2001; Kohler, Crane, & Milner, 2002; Nakamura, Kawashima et al., 2000); 6. letters (Gros et al., 2001; Polk et al., 2002); and 7. words (Cohen, Jobert, Le Bihan, & Dehaene, 2004). Many of these categories, such as living and non-living stimuli, are studied in normal healthy adults in response to the aforementioned cases of related category-specific deficits. In healthy adults, researchers consistently find left hemisphere correlates for non-living items regardless of task or contrast stimuli. For example, in naming, viewing, and matching tasks, tools (non-living stimuli) have been contrasted with other object stimuli as well as with stimuli of living things. Via positron emission tomography (PET) (Martin et al., 1996; Perani et al., 1999) and fMRI technology (Chao & Martin, 2000), left premotor, left middle temporal, and left posterior parietal regions have been identified as neural substrates for tools. In addition to neural correlates of non-living things, neural substrates for living things are also reported (Leube et al., 2001; Martin et al., 1996). In a fMRI semantic categorization task, the right fusiform gyrus, middle temporal gyrus, and inferior frontal gyrus were significantly activated in response to living versus non-living word categories (Leube et al., 2001). Fusiform activation in response to living stimuli (i.e. animals) versus non-living stimuli (i.e. tools) was also reported by Perani et al. (1999) though in the opposite hemisphere. Thus, separate cortical processing regions for non-living and living things in normal functioning individuals support the argument for domain-specificity.

Beyond the superordinate category levels of living versus non-living things, researchers report neural substrates dedicated to processing more specific taxonomic categories. Multiple imaging studies employing a wide variety of tasks report a neural correlate for face processing, a mid-anterior fusiform area, called the fusiform face area (FFA) (Kanwisher et al., 1997). PET studies using same/different matching tasks, (Gorno-Tempini & Price, 2001) discrimination tasks (Nakamura, Kawashima et al., 2000), and passive-viewing tasks (Sergent et al., 1992) report significantly greater responses to faces than comparison stimuli in the mid-fusiform gyri. Functional MRI investigations also report a similar face-sensitive region where faces produce significantly greater activation than hands (Kanwisher et al., 1997), houses (Kanwisher et al., 1997), scrambled stimuli (Kanwisher et al., 1997; Puce et al., 1995), and scenes (Kanwisher et al., 1999). Despite the orientation (Kanwisher et al., 1997; Kanwisher, Tong, & Nakayama, 1998), the type (i.e. mooney faces) (Andrews & Schluppech, 2004), or the degree of familiarity (Gorno-Tempini & Price, 2001; Nakamura, Kawashima et al., 2000) of the face stimulus, the mid-fusiform region is consistently activated by face stimuli relative to other categories. Though other regions have been identified as face-responsive and may serve as neural correlates for face processing (Gauthier, Tarr et al., 2000; Puce et al., 1995), consistency across studies, contrasting categories, and stimulus presentation provide strong evidence for the mid-fusiform region, particularly the right mid-fusiform (Gorno-Tempini & Price, 2001; Kanwisher et al., 1997; Nakamura, Kawashima et al., 2000), as a neural correlate of face processing.

Similar to faces, evidence exists for a cortical region specialized to visually process body parts. In a passive-viewing fMRI experiment, Downing et al. isolated a right lateral occipital region that was highly responsive to body parts relative to other stimuli (i.e. whole faces, face parts, whole objects, object parts, and mammals) whether body parts were presented as line drawings, photos, silhouettes, or stick figures (2001). This “extrastriate body area” (EBA) is presumed a dedicated neural module for visually processing body part stimuli. In addition to neural correlates of face and body part processing, cortical regions have been shown to respond preferentially to places and scenes. Using PET (Gorno-Tempini & Price, 2001; Nakamura, Kawashima et al., 2000) and fMRI (Epstein et al., 1999; Kohler et al., 2002), the bilateral "parahippocampal place area" (PPA) (Epstein et al., 1999) has been repeatedly identified as responding significantly more to buildings and scenes than other stimuli. Cortical regions for letter and word processing have also been identified. In a fMRI passive viewing task with strings of consonants, digits, and shapes as stimuli, Polk et al. found a left fusiform region more sensitive to letters than digits (2002). In another passive viewing fMRI task, Gros and colleagues identified a similar left hemisphere neural substrate for single letters (2001). An active matching task produced the same results (Polk et al., 2002). Beyond letters to words, PET (Leff et al., 2001; Petersen et al., 1990) and fMRI (Cohen et al., 2004) research indicate visual word form areas located in the region of the left occipito-temporal junction. The existence of letter and word-responsive regions indicates postnatal category-specific development of the cortex. Collectively, these neuroimaging findings in normal, healthy individuals support lesion study data indicating a domain-specific functional organization of the cortex.

In addition to imaging studies, physiological studies (Bentin, Allison, Puce, Perez, & al., 1996; Liu, Higuchi, Marantz, & Kanwisher, 2000) have identified face-responsive cortical regions in normal adults. Using event-related potentials (ERPs) to assess neural responses to human faces, animal faces, and objects, Bentin and colleagues reported a negatively deflected potential to the onset of face stimuli at 170ms post-stimulus (N170). This N170 consistently occurred in response to human face stimuli whether faces were upright, inverted, familiar, or unfamiliar. Thus, ERP studies indicate a temporal correlate for face processing in conjunction with confirmation from fMRI and PET studies of a spatial correlate for faces. To evaluate both spatial and temporal correlates of face and non-face stimuli in normal adults, Liu et al. used magnetoencephalography (MEG) (2000). An M170 response to photos of faces corresponded to the 170ms potential of ERP studies and the occipito-temporal locus of fMRI studies.

At a different level, single-neuron recordings have revealed category-specific responses to faces, natural scenes, houses, and animals in human medial temporal cortex (Krieman, Koch, & Fried, 2000). Supporting single-cell findings of category differentiation, Fried and colleagues found single neurons in the same medial temporal area that discriminated faces from inanimate objects (1997). Thus, in healthy adults, neuroimaging and physiological data point to the existence of a domain-specific modular organization of visual processing.

Normal Healthy Children

At the inception of this project, developmental neuroimaging and physiological literature regarding the functional organization of the ventral processing stream in normal children was limited. The majority of research concerning the neural correlates of face and object processing has been conducted in adults and in impaired children (i.e. autistics and developmental prosopagnosics) (Bar et al., 2001; Downing et al., 2001; Haxby et al., 1994; Kanwisher et al., 1997; Kendrick et al., 2001; Nakamura, Honda et al., 2000; Sergent et al., 1992). Though developmental imaging literature in face and object processing is increasing, information on the subject is still minimal. Here, the few new and existing studies relevant to the functional development of normal face and object processing in children are discussed.

In addition to our findings explained in detail later in this work (see Chapters 4-6), two functional magnetic resonance imaging studies of normal face and object processing development exist. Most recently, Aylward et al. (2005) focused on activation patterns in the fusiform gyrus for two age groups of children (younger, 8-10 years and older, 12-14 years) viewing two categories of stimuli, faces and houses. A significantly greater response to faces than houses emerged in the bilateral fusiform gyri of the older children but not in younger children. These results suggest an increase in categorical differentiation and, therefore, an increase in domain-specificity with age. Second, Passarotti and colleagues used a face-matching task to compare VPS patterns of functional activation in children ages 10-12 years and adults (2003). Their results indicated that children had a more distributed pattern of activation (i.e. more activation lateral and anterior to the classically defined fusiform face area) in the fusiform gyrus than adults. From the data, it may be concluded that the basic functional organization of the VPS continues to adapt and become more specialized with age. Thus, evidence of a developmental decrease in the distribution of neural activation within a stimulus category and maturational increases in differentiation between categories may be seen as supporting an increasingly domain-specific neural network.

A limited number of electrophysiological studies have also explored the development of face and object processing. As indicated in the fMRI data, the functional organization of the VPS may undergo specialization with age. In their infant ERP study, de Haan and colleagues used a passive viewing procedure to investigate the development of cortical specialization in face processing (de Haan, Pascalis, & Johnson, 2002). ERPs were recorded while six month olds and adults viewed human and monkey face stimuli in upright and inverted orientations. In adults, a face-specific negative going potential, the N170, was unique in its response to upright human faces. In contrast, no infant potentials demonstrated sensitivity to species and orientation of faces. In a study of 3 month and 12 month old infants, Halit, de Haan, and Johnson evaluated two face-sensitive infant ERPs (N290 and P400) for maturational changes in the specificity (2000). In response to monkey and human faces, both face sensitive components increased in their specificity for human faces by 12 months. No specificity was seen at three months. Together, these developmental differences in specificity indicate a narrowing of neural processes for face processing. As these studies were limited to face processing, their results can only speak to developmental specialization within the category of faces. Conversely, Carver et al. investigated the maturation of face processing relative to object processing across three age groups (18-24 months, 24-45 months, and 45-54 months) using pictures of familiar and unfamiliar faces and toys as stimuli (2003). Results revealed that children's responses to familiar and unfamiliar faces but not objects varied as a function of age. The youngest children showed greater ERP responses to familiar faces than unfamiliar whereas the oldest children showed greater responses to unfamiliar faces. Twenty-four to forty-five month old children showed no differential responses to faces. From their findings, Carver and colleagues concluded that developmental changes in processing are unique to faces relative to toys. Thus, face processing is special and specialized within the VPS.

Investigations in Other Species

Neural correlates of face and object recognition have been examined in other species. Primate studies also exist that support selective modules of visual processing. A population of inferior temporal cortex cells in the brains of the rhesus Macaque produced a selective response to faces (Wang, Tanifuji, & Tanaka, 1998) and a subset of these cells responded selectively to specific facial features (Perrett, Rolls, & Caan, 1982). In addition to monkeys, evidence for domain-specificity is reported in studies of sheep. Using single-cell recordings, Kendrick et al. explored the possibility that sheep have specialized face processing regions (2001). The sheep data indicated small populations of cells in the temporal and medial prefrontal cortices encoded faces as opposed to other visual stimuli. Thus, domain-specific organization is supported across species.

“Specific” Summary

In disordered human brains and normal brains of humans, monkeys, and sheep, domain-specificity has been investigated using a wide range of techniques. Proponents for a modular VPS neural blueprint build their models of the mind on the basis of evolutionary history (Capitani et al., 2003). Domain-specific regions are a plausible response to the need for quick and efficient processing of the environment for survival (Capitani et al., 2003). Therefore, domains for faces (Kanwisher et al., 1997), places (Epstein, DeYoe, Press, Rosen, & Kanwisher, 2001), inanimate biological objects (e.g. vegetables and fruits) (Capitani et al., 2003), and artifacts (e.g. tools) (Martin & Weisberg, 2003; Moore & Price, 1999) seem logical explanations for the findings discussed above.

Domain-General Organization

From the extent of literature presented here, it would seem that domain-specificity has much support. However, domain-generalists cite weaknesses and contrary evidence and explanations.

Prosopagnosia

As in the case of domain-specificity, findings from some lesion and disorder studies support a domain-general system (Damasio et al., 1982; Damasio, Tranel, & Damasio, 1990; de Gelder & Rouw, 2000b; Gauthier, Curran, Curby, & Collins, 2003). In fact, Gauthier, Behrmann, and Tarr argue that current prosopagnosia literature lacks evidence for pure face versus non-face impairments citing multiple prosopagnosia cases in which deficiencies existed in both face and object processing (1999) (c.f. Duchaine & Nakayama, 2005). To support their criticism, Gauthier and colleagues tested two prosopagnoiscs for true categorical deficits. Comparing two prosopagnosics with controls on object discrimination tasks (objects were from multiple categories, face and non-face), the investigators found that, unlike controls, subject performance was more affected by manipulations within category domains than between categories. The finding of impaired recognition performances at the subordinate level across many categories rather than impaired recognition of one-specific category (i.e. faces) challenges the neuropsychological evidence for domain-specificity, specifically the existence of a face-specific module.

Similarly, by examining reported cases of recognition defects, Antonio Damasio (1990) noted that most recognition breakdowns occurred at the subordinate level irrespective of categorical boundaries or lexical labels. From this, he concluded that the recognition system was not organized on the basis of conceptual categories but around sets of shared perceptual features and interactions (Damasio, 1990). In yet another case, Barton and colleagues studied perception in three patients with developmental prosopagnosia and found that, though all were deficient on face matching tasks, their impairments were not limited to faces (2003). All three subjects also had trouble on other “within-category” judgments. Thus, the prevalence of convoluted rather than pure agnosias along with findings of within-category deficits contribute to a more general rather than domain-specific theory of VPS organization.

Other Disorders

Capitani, et al. (2003) conducted an exhaustive review of the clinical cases of semantic category-deficits (with the exception of developmental cases) and found little reliable evidence supporting category-specific agnosia or anomia. Overall, the clinical cases revealed a disproportionate impairment in one category versus another rather than the presence of a selective impairment. Of the seventy-nine complete and useable cases the authors reviewed, sixty-one were disproportionately impaired for biological categories and eighteen were disproportionately impaired for artifacts. Results of Capitani et al.’s review concur with Gauthier and others prosopagnosia findings that cases of category-specific object processing deficits are frequently accompanied by deficits in other categories. Furthermore, in attempting to define what categories are involved in specific deficits, Capitani et al. proposed a very broad classification including animate objects, inanimate biological objects, and artifacts. These broad groupings are composed of overlapping classes of objects and members of these groupings can be filed in more than one category (e.g. faces are both animate and biological). Thus, such minimal evidence for true domain-specific deficits in accounts of object recognition along with impaired face recognition support overlapping rather than compartmentalized organization of the ventral processing stream.

Normal Healthy Adults

Among visual recognition studies in healthy adults, several investigations support overlapping face and object neural networks rather than domain-specific modules. For example, in an fMRI study using houses, chairs, and faces, Ishai et al. (1999) found cortically distributed rather than segregated regions for face processing. Distinct VPS regions responded preferentially to each category (i.e. 3 face regions, 1 house region, and 1 chair region) yet each region also responded significantly to the other classes of stimuli. Ishai and colleagues concluded that recognition processing was not restricted to maximum responsive regions but distributed across cortex with each category having its own differential pattern of responses in the VPS (Ishai et al., 1999).

As further support for domain-general organization, several studies found category-sensitive rather than category-selective neural responses. In a visual matching positron emission tomography (PET) study using famous versus non-famous buildings and faces results indicated significant activation of the right fusiform gyrus, the "fusiform face area", by all types of faces (Gorno-Tempini & Price, 2001). But this same area was also activated by pictures of buildings. Activation of the right fusiform gyrus by buildings as well as faces implicates a sensitive but not selective response in this region. Similarly, another study determined the extent to which regions associated with face processing were selective for faces by examining fMRI responses to human faces, dog faces, houses, and scrambled images (Blonder et al., 2004). Blonder et al. (2004) concluded that the lateral fusiform gyrus, an area corresponding to the fusiform face area (e.g. Kanwisher, 1997), was face sensitive but not face selective as it responded significantly to both faces and houses.

Furthermore, sensitive rather than exclusively selective activation of the visual processing system as a whole is supported by an fMRI study involving matching inverted and upright houses and faces. This study defines selectivity as relative differences in the response to these two categories and not relative to other visual stimuli. Based on this definition, the study identifies multiple bilateral areas of "selectivity" for houses and faces, including areas within the fusiform gyri and the occipital lobe (Haxby et al., 1999). Multiple regions of selectivity for each type of stimulus are indicative of connected regions or processing pathways -- not individual processing modules. Also, the authors reported that both face-selective and house-selective areas were activated (degrees of significance varied) by inverted forms of the opposing stimuli and that face-selective regions responded less to upright faces than house-selective areas responded to upright houses (Haxby et al., 1999). In other words, “selective” areas are numerous for each stimulus and their selectivity is based on graded amounts of activation between houses and faces rather than exclusive activation. This supports Ishai and colleagues’ conclusion that overlapping regions function in the similar processing of objects and faces.

These neuroimaging studies have documented sensitive neural substrates which respond differentially to multiple stimulus categories rather than responding exclusively to one category. Discrepancies in these findings with data supporting domain-specificity may be founded in the definition and assessment of “selective activation” (Joseph et al., 2002). Frequently, brain imaging studies fail to address the distinction between a selective and a differential response to stimuli. Selective activation refers to a statistically significant response to one condition relative to all other experimental conditions and all other conditions produce statistically equivalent responses to one another. In other words, a selective brain region responds exclusively to one experimental condition (i.e. face-selective regions produce only a significant response to faces and no other stimuli). Differential activation, in contrast, is defined by a statistically greater response to one condition relative to all others but one or more of the other conditions also generate a response greater than baseline. For example, a face-differential region is more responsive to faces than other categories but not exclusively responsive to faces. Selective activation is the basis for domain-specific views whereas differential responses support the domain-general account of functional organization. Thus, it is critical that functional imaging studies carefully distinguish among different activation patterns. The common use of analysis techniques, subtraction and conjunction, limited in their assessment of differential brain patterns (Joseph et al., 2002) may be the basis for controversial findings of category-specific regions. Further assessment of data may be needed to verify truly selective neural substrates.

Primate Studies

Again, interspecies studies contribute to the controversy surrounding the functional organization of the VPS. A study of rhesus monkeys in which "face-selective" superior temporal cells were surgically removed, found general visual impairments rather than face-specific deficits (Eacott, Heywood, Gross, & Cowey, 1993) *indicating* general processing regions in which face and object neural correlates overlap.

"General" Summary

Strong arguments for each side of the neural architectural debate exist. From these investigations, it is apparent that the question of how the VPS is organized is yet unresolved across health, age, and species. If the collection of existing data indicates a domain-general organization of the VPS, then what, if not category, determines the functional organization underlying face and object processing?

Gauthier and colleagues proposed an experienced-based expertise model for these regional variations in neural sensitivity to stimuli. Using novel objects called greebles, Gauthier et al. found increased fMRI signal in the mid fusiform gyrus (i.e. the fusiform face area, (Kanwisher et al., 1997) as expertise for the stimuli increased. Thus, this area was not selectively involved in face processing (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999) but amplitude of signal was related to experience with the category. Applying this to the findings of Ishai (1999), Haxby (2001), Blonder (2004) and others (Chao, Haxby, & Martin, 1999) expertise explains graded sensitivity to faces, houses, and chairs, stimuli humans frequently encounter in the environment.

2.) What are the underlying cognitive mechanisms?

Face processing: Are Faces Special?

Are faces like other classes of objects or are they unique? Not only does a debate exist regarding the functional organization of visual processing in the VPS but, the cognitive mechanisms that drive face and object processing are also debated. There is division among face perception researchers on the topic of whether or not faces are special. Adult studies and studies of face processing disorders, as discussed previously, contribute to both sides of this argument. Developmental data deepen the controversy. In contrast to the relatively limited number of healthy developmental fMRI studies, behavioral information regarding infant and child face processing is prevalent. However, results and interpretations are varied. In addition to the aforementioned literature supporting face-specific deficits (prosopagnosia) and face-selective brain regions (e.g. FFA, Kanwisher et al., 1997), three lines of evidence exist for the argument that faces are a special category of stimuli: 1.) infant preferences for faces; 2.) differential effects for face and object recognition with orientation; and 3.) face-specific developmental changes in recognition performance.

Newborns show a preference for face-like patterns versus other patterns (Johnson & al., 1991; Morton & Johnson, 1991). Based on this and other behavioral findings, Farah and others propose that infants and children have a “face” mechanism (1996; 2000; Johnson & al., 1991; Morton & Johnson, 1991) (and possibly a neural module) that directs their attention to faces. However, other researchers interpret the newborn’s face preference to indicate the existence of a general perceptual mechanism pre-wired for specific visual patterns (Turati, 2004).

In addition, those who argue that faces are a special category of stimuli emphasize that faces are disproportionately affected by orientation relative to other non-face stimuli. Scientists refer to this orientation phenomenon as the face inversion effect. Many interpret poorer recognition performance on inverted faces relative to other orientation and stimuli as a qualitative difference in face and object processing (Bartlett & Searcy, 1993; Carey & Diamond, 1977; Carey & Diamond, 1994; Diamond & Carey, 1986; Freire, Lee, & Symons, 2000; Maurer, Le Grand, & Mondloch, 2002; Murray, Rhodes, & Schuchinsky, 2003; Searcy & Bartlett, 1996; Tanaka & Farah, 1993; Valentine, 1988; Young, Hellawell, & Hay, 1987). Though, most investigators agree that the inversion effect does denote differential processing between faces and objects, some argue that the differences are quantitative not qualitative in nature (Maurer et al., 2002; Reed, Stone, Bozova, & Tanaka, 2003; Want, Pascalis, Coleman, & Blades, 2003). Whether qualitative or quantitative, the differences in face and object processing revealed by the face inversion effect become more pronounced with age (Diamond & Carey, 1986). This developmental difference supports the third line of evidence that faces are indeed special.

Proponents of the special status of faces cite that cognitive mechanisms for face recognition change from childhood to adulthood, whereas processing of objects remains relatively constant across one’s lifespan (Farah, 1996; Ward, 1989). Unlike the controversy surrounding face recognition, much research supports the conclusion that object recognition is similar in childhood and in adulthood. Developmental studies indicate the presence of adult-like mechanisms for categorization in 3 to 4 month old infants (Quinn, Eimas, & Tarr, 2001). Also like adults, at three months, infants display sensitivity and selective attention to information relevant to 3-D structural processing (Bhatt & Bertin, 2001; Bhatt & Waters, 1998). Furthermore, Ward (1989) documents the use of adult-like object recognition strategies by 5 years of age. However, controversy exists over the similarity of face recognition among these age groups. Still other studies in healthy and disordered individuals deny category-based perceptual processing differences in children and adults. Those who oppose the "special" status of faces explain age-related changes in face recognition skills as functions of expertise or the maturation of general cognitive factors such as attention and memory rather than developmental changes in perceptual processing mechanisms (Baenninger, 1994; Gilchrist & Mckone, 2003; Pellicano & Rhodes, 2003; Pezdek, Blandon Gitlin, & Moore, 2003; Turati, 2004; Want et al., 2003).

In the midst of these two opposing views, how is one to determine if the "special" status of categories and, therefore, domain-specificity exists? Ramsey and Langlois (2002) make note of two criteria that must be met before assigning a "special" label to faces:

1.) a specific mechanism must exist that directs an individual's attention toward faces (more than toward non-face stimuli) and that processes facial information

2.) individuals must respond to faces in a qualitatively different manner than to other non-face stimuli

These two conditions can be applied to face and non-face categories to address the question of "specialness" and underlying processing mechanisms. In addition to behavioral criteria, neuroimaging and physiological investigations can be used to assess the claims of category-specific mechanisms and corresponding neural substrates.

Faces Are Special

Innate Face Mechanism

Does a specific mechanism exist that directs an individuals attention toward faces and that processes facial information?

Even in infancy faces are special. Newborns prefer faces over other objects (Goren, Sarty, & Wu, 1975; Mondloch & al., 1999; Nelson, 1987) (see review Nelson & Ludemann, 1989). For example, Goren et al. (1975) and later Johnson et al. (1991) found that within 30 minutes of birth newborns track schematic faces farther than other non-face stimuli. From this preference for faces, Johnson et al. (1991) speculated that even at birth faces have an advantage over other non-face stimuli so that infants are born with an innate face mechanism that predisposes them to attend to facial patterns (Morton & Johnson, 1991). This mechanism is known as CONSPEC. In theory, CONSPEC uses inputs from a lower functioning subcortical region of the brain, the retinotectal pathway. In addition, Johnson et al. found that the infant's preference to faces disappears at 1-2 months and reappears by 2-3 months. Based on this preference phenomenon, they proposed a second more mature face-specific mechanism, CONLERN. Unlike CONSPEC, CONLERN is mediated by higher cortical functions via the retinocortical pathway and develops from experience with faces.

The existence of this innate mechanism for face processing is also supported by a developmental prosopagnosia study in which a 16-year old individual, Adam, who sustained brain damage one day after birth presented with a disproportionate impairment in face to object recognition (Farah et al., 2000). Neuropsychological testing revealed that Adam identified real objects without difficulty. In contrast, he performed with difficulty on photos and line drawings of objects, particularly line drawings of living things (i.e. animals and plants). Hence, though Adam's object recognition system was compromised, it was functional. On the other hand, Adam's face recognition system was non-functional. Face recognition tasks revealed a profound impairment with Adam unable to identify any familiar or famous faces. In their investigation, Farah et al. (2000) concluded that the lack of compensation for face processing by the existing object recognition system indicated a distinct and innate face-specific mechanism.

Human infant studies, lesion studies, as well as studies in other species indicate innate visual recognition pathways. In their comparison of the visual structures and pathways in amphibian, avian, rodent, and primate species, Sewards and Sewards (2002) confirmed the existence of an innate subcortical visual recognition system used to overtly discriminate biologically relevant objects. In the first few months of a primate's life (human and non-human) visual object recognition shifts entirely from this innate subcortical system to an experienced-based cortical system. Seward and Seward's review is in line with Morton & Johnson's proposal of innate face-specific mechanisms. From each of these studies one can recognize the theme that faces are special – innately special.

Qualitative Differences – Inversion Effect

Do individuals respond to faces in a qualitatively different manner than to other non-face stimuli?

Studies of infant face preferences are only a small portion of the evidence for the special status of faces. The idea that faces are processed differently from objects is also supported by studies of orientation effects on faces versus other non-face stimuli. From around ten years to adulthood, inversion affects recognition of faces more than other object stimuli (Yin, 1969) implying that face processing varies from object processing. In addition to inversion, other experimental manipulations (e.g. composite effect) (Carey & Diamond, 1994) indicate that the type of information used for face recognition differs from that used for object recognition.

Several hypotheses exist concerning face processing and all of these have empirical support. The **feature hypothesis** (or analytical hypothesis) proposes that faces are perceived and remembered based on individual attributes (e.g. nose, mouth, eyes) without regard to relationships among the attributes (Cohen, 1998). Two other hypotheses are referred to as "relational." Unlike the feature-based hypothesis, the holistic hypothesis stresses an advantage for recognizing the face part in the context of the whole face rather than in isolation (Tanaka & Farah, 2003). The **holistic hypothesis** proposes that faces are recognized based on a certain perceptual "wholeness" where features and inter-featural information are perceived as a single entity, a gestalt representation (Baenninger, 1994; Farah & al., 1998; Tanaka & al., 1998; Tanaka & Farah, 1993). In addition to holistic processing, configural processing is also relational rather than featural. Two types of configural information exist -- first order (general relational order of features, e.g. eyes above nose and nose above mouth) and second order (spatial relationships between features, e.g. distance between eyes or distance from nose to mouth) (Diamond & Carey, 1986). The **configural hypothesis** of face processing proposes that faces are distinguished from one another on the basis of their second order information. First order configural information is common to all faces but second order information is unique to each individual face. With regards to these hypothesis, inversion has been shown to differentially affect relational (i.e. holistic and configural) processing (Bartlett & Searcy, 1993; Carey & Diamond, 1977; Carey & Diamond, 1994; Diamond & Carey, 1986; Freire et al., 2000; Maurer et al., 2002; Murray et al., 2003; Searcy & Bartlett, 1996; Tanaka & Farah, 1993; Valentine, 1988; Young et al., 1987). The phenomenon of poorer recognition performance on inverted versus upright stimuli is known as the inversion effect (see Valentine, 1988). Inversion disrupts relational processing and faces are more vulnerable to inversion than other non-face categories (Yin, 1969). Therefore, face recognition relies more on relational processing than does object recognition. These processing differences determined by orientation imply that face and object recognition mechanisms are qualitatively different (Murray, Yong, & Rhodes, 2000).

Qualitative Developmental Changes

Developmental changes documented in face processing but absent in object processing point to the uniqueness of faces. In their initial studies, Carey and Diamond demonstrated a shift in unfamiliar face recognition capabilities between six and ten years of age (1977; Diamond & Carey, 1977). Performing equally well on upright and inverted house and face recognition memory tasks, six-year-olds showed no evidence of the face inversion effect. In contrast, 10 year old children performed better on upright than inverted faces (Carey & Diamond, 1977). A similar inversion effect was not seen in object processing at any age. In the same study, the authors tested children's recognition performance by manipulating features (i.e. distracting versus helpful paraphernalia) on model faces. Six year olds but not 10 year olds were easily fooled by the feature changes. Based on the two experiments, Carey and Diamond credited the lack of an inversion effect in younger children to feature-dependent recognition of unfamiliar faces whereas the occurrence of a face inversion effect in older children indicated an age-related reliance on relational information for face processing. These data resulted in the "encoding switch" hypothesis which proposed a mechanistic change in face recognition from a feature-based to a configural strategy around 10 years of age. Similarly, Schwarzer (2000) proposed different mechanisms of face recognition for upright stimuli in children and adults. To differentiate between relational and featural face processing strategies, Schwarzer tested 7 year olds, 10 year olds, and adults on a category learning test. Participants learned to place schematic faces in one of two categories based on feedback regarding either a featural or relational characteristic. Following the learning phase, subjects were tested on additional versions of either inverted or upright face stimuli. Based on the subjects' categorization assignments, Schwarzer could identify whether a featural or relational strategy was used. She reported that 7 year olds preferred featural processing of faces in both orientations while 10 year olds and adults preferred relational processing for upright faces (Schwarzer, 2000). Furthermore, adults processed inverted faces featurally. Schwarzer's category learning task with faces was an adaptation from a developmental object processing study by Ward (1989). Ward found a featural dominance in non-face object processing from 5 years to adulthood. Thus, no developmental shifts occurred for visual processing of non-face objects. As a group, these studies point to a developmental shift unique to face processing mechanisms.

In a series of later studies, Carey & Diamond modified their hypothesis. Using the composite task in which the top-half of a face from one person is combined with the bottom half of another person's face, Carey and Diamond assessed recognition naming performance in 6 year olds, 8 year olds, and adults (1994). In the task, composite and non-composite faces appeared in upright and inverted orientations. As composite stimuli produce new face configurations, the authors reasoned that poorer performance on composite than non-composite tasks infers the use of relational processing. In contrast, featural processing, unaffected by the creation of new configurations, is evidenced by similar performance on composite and non-composite trials. Results indicated that 6-year olds, 10-year olds, and adults used relational processing for upright faces. The use of relational information for upright face recognition in six year olds conflicted with Carey and Diamond's earlier conclusion that younger children (less than 10 years) used featural processing for upright faces. Inversion findings, however, were similar between the two studies. Six year olds continued to perform equally well at either orientation implying some reliance on featural processing whereas 10 year olds and adults continued to perform better on upright than inverted stimuli implying the use of relational processing. In light of their finding that children as young as six years of age use relational information for upright face recognition, Carey and Diamond explained the age-related inversion effect as an experienced-based bias for relational processing of normally-presented upright faces. In other words, the "norm-based" encoding switch involves an increased reliance on relational processing relative to experience with a prototypical face. In line with these more recent findings of Carey & Diamond, Thompson et al. showed that 7-month old children may be sensitive to second order relational properties of faces (2001). This study implies that even very young children have the capacity to use second order relationships in face processing. Thus, children are capable of relational processing but the extent to which they implement it when viewing faces differs from adults. Additional studies have noted this developmental shift in face processing mechanisms from a greater reliance on features in childhood to a greater reliance on relational information (configural/ holistic) in adulthood (Carey & Diamond, 1994; Freire & Lee, 2001; Freire & Lee, 2003a; Mondloch, Geldart, Maurer, & Le Grand, 2003; Mondloch, Le Grand, & Maurer, 2002; Schwarzer, 2000). In summation, developmental studies support the special status of faces by demonstrating that processing mechanisms for faces, unlike those for non-face objects, undergo maturational changes.

Faces Are Not Special

If faces are not special then what explanations can be found for infant preferences, orientation effects, and developmental shifts? Proponents of domain-general cognitive theories speak of quantitative differences in face and object processing due to the maturation of general cognitive abilities and experience-based expertise rather than different mechanisms.

Innate Perceptual Mechanism

Despite evidence in infant, lesion, and interspecies studies, the domain-specific idea that there is an innate brain mechanism devoted to processing faces is not universally supported. Many researchers support a face-preferential response in newborns (Goren et al., 1975; Johnson & al., 1991; Valenza, Simion, Cassia, & Umilta, 1996) (c.f. Easterbrook & al., 1999) but the interpretation of this preference for faceness is controversial. In contrast to a visual system innately tuned to faces, newborns' systems may be tuned to general properties of perceptual processing. Turati et al. explored the idea of a domain-general explanation for infant face preferences by monitoring newborns' looking times to two different nonspecific perceptual properties typical of faces but found in other non-face stimuli, up-down asymmetry and congruency (2004). For up-down asymmetry patterns more elements occur in the upper than lower part of a stimulus shape. For congruency, the greater number of inner elements is located in the widest part of a stimulus shape. Results demonstrated that an up-down asymmetry not faceness guided infants looking preferences. This implies that infants are predisposed to particular visual patterns not to particular visual categories. Hence, Turati et al. argue for an innate perceptual mechanism and against an innate face mechanism.

Quantitative Differences – Inversion Effect

Not only does the special status of faces hinge on the existence of a face-specific processing mechanism but this mechanism must be qualitatively different from that of other object categories. As mentioned previously, many studies support a qualitative difference in the processing of faces relative to other object stimuli (Bartlett & Searcy, 1993; Carey & Diamond, 1977; Carey & Diamond, 1994; Diamond & Carey, 1986; Freire et al., 2000; Maurer et al., 2002; Murray et al., 2003; Searcy & Bartlett, 1996; Tanaka & Farah, 1993; Valentine, 1988; Young et al., 1987). This qualitative difference in face processing is based primarily upon studies of orientation effects on faces versus other non-face stimuli.   Face recognition performance is differentially hampered by stimulus inversion and inversion effects relational (holistic and second-order configural) processing. Therefore, faces are deemed special in that face recognition involves more relational processing than other object categories. However, data exists to the contrary.

Three lines of reasoning explain opposing findings to qualitative processing differences between faces and objects (Gauthier, Anderson, Tarr, Skudlarski, & Gore, 1997; Maurer et al., 2002; Reed et al., 2003; Want et al., 2003). First, stimulus inversion has been accepted as a standard test for determining qualitative processing differences based on the assumption that inversion affects relational processing. Under this assumption, claims have been made that faces alone are disproportionately affected and therefore, are a unique category (Yin, 1969). However, Maurer, LeGrand, & Mondloch reject the inversion test as the gold-standard of quality changes in processing mechanisms citing that the inversion of faces interferes with first-order and second-order configural processing as well as holistic and even featural processing (2002). Thus, the inversion effect alone in not sufficient for determining a particular type of face processing nor can it attest to the processing differences between faces and objects (Maurer et al., 2002). Secondly, in proclaiming that faces are special, many studies have investigated inversion effects in faces only and have failed to investigate inversion effects on other object categories (Want et al., 2003). Without a comparison basis, changes in face recognition can not be credited as face-specific. A third, and related, oversight often exists in the investigations of face processing. Not only do many studies fail to test other non-face categories, but those studies that include objects often fail to make direct stimulus comparisons by constraining object categories to those in which, like faces, exemplars are structurally similar to each other (Gauthier et al., 1997; Maurer et al., 2002; Reed et al., 2003; Tarr, 2003). The following studies have addressed these deficits and found quantitative rather than qualitative distinctions in face and object processing mechanisms.

Using response classification techniques, Sekuler et al. (2004) determined the perceptual strategies underlying processing for upright and inverted faces. The response classification technique reveals the parts of a stimulus used to make a decision by introducing variations of external noise on a trial by trial basis and measuring response bias. Though this study found significantly greater impairments on inverted than upright faces, no qualitative processing differences coincided with orientation. For both upright and inverted face discrimination, results indicated that participants used highly localized regions near the eyes. Thus, efficiency not strategy varied with orientation.

By discrediting the idea that face inversion produces qualitative changes in processing strategies, Sekuler et al. provided data for the argument that faces are not special. However, their investigation was limited to effects within the category of faces. In a prior study, Gauthier and Tarr challenged the idea of a face-specific region and corresponding mechanism by testing subjects' performance on inverted and upright novel objects called greebles (1997). Greebles, 3-D computer generated complex objects, are visually similar in regards to the number and configuration of their parts. In this way, like faces, greebles are a homogenous group of stimuli (Gauthier & Tarr, 1997). Results revealed an inversion effect for greebles similar to that of faces. This disruption of object recognition by inversion, contributes to evidence against a qualitatively unique face mechanism. Gauthier proposed that experience within a homogenous class of stimuli rather than taxonomic category explained the special status of faces.

Findings by Reed and colleagues further discredit the special status of faces. Recognition performance of upright and inverted faces, houses, and body positions was compared using a same/different behavioral task (2003). This study compared face and non-face object classes as well as a direct comparison of two object categories with structurally similar exemplars (i.e. faces and body positions). In contrast to the Gauthier and Tarr study of novel objects (1997), subjects were not trained on the task. Reed et al. found that while houses differed from the other two categories, inversion affected recognition of faces and body positions similarly (2003). Faces and body positions are distinctly different categories but possess similar within class characteristics. Thus, this finding refutes the existence of a face-specific mechanism and points rather to a mechanism based on experience and / or structural similarity.

Quantitative Developmental Changes

Across developmental face studies, findings support maturational changes in recognition. However, as in adult inversion studies, scientists disagree whether changes are qualitative (Carey & Diamond, 1977; Carey & Diamond, 1994; Schwarzer, 2000) or quantitative (Baenninger, 1994; Itier & Taylor, 2004a, 2004b; Pellicano & Rhodes, 2003; Pezdek et al., 2003; Sangrigoli & de Schonen, 2004) in nature. As previously established, faces are not special if there is no qualitative difference between face and object processing. In one behavioral and two ERP studies involving upright, inverted, and contrast-reversed unfamiliar face stimuli, Itier and Taylor investigated the role of configural changes in development and the effects of memory on face recognition from eight to sixteen years of age (2004a; 2004). Behavioral and ERP results on an n-back repetition task revealed an improvement in upright face recognition with age as well as an age-related improvement on negative and inverted faces. Contrary to other studies (Carey & Diamond, 1994; Schwarzer, 2000), the inversion effect, occurring in 8 year olds, did not increase with age. Based on the finding of an early inversion effect, Itier and Taylor inferred the emergence of configural processing by 8 years of age. Furthermore, as the inversion effect did not increase with age, the authors argued against an encoding shift. Analysis of the repetition aspects of the task revealed improved memory and reaction time with age. Thus, Itier and Taylor suggest a quantitative change in face processing with age based on maturation of working memory processes.

Quantitative changes in face processing have also been ascribed to attention maturation. In a paraphernalia study, children, four to seven years of age, participated in a series of face recognition tasks (Freire & Lee, 2001). Using face stimuli differing in either featural or second-order configural information, Freire & Lee found that 4 year olds and 7 year olds performed well on featural and configural trials (2001). In the learning target/non-target face recognition task, Friere and Lee found that inclusion of paraphernalia diverted attention away from the face itself. In addition, paraphernalia effects were greater in younger children than older children. Together, Friere and Lee's findings indicate that developmental changes in attention, rather than perception mechanisms, may contribute to age differences in face recognition. Thus, developmental studies, both physiological and behavioral, provide evidence for quantitative rather than qualitative differences in face processing with age. Their findings imply developmental differences based on changes in general cognitive mechanisms such as memory (Itier & Taylor, 2004a, 2004b; Itier & Taylor, 2004) and attention (Freire & Lee, 2001; Freire & Lee, 2003a) as opposed to changes in perceptual mechanisms.

Similarly, in another face recognition study, Baenninger found no developmental differences in face recognition styles between children (six and eleven years) and adults (1994). Direct manipulation of the internal configuration of faces in a forced choice matching task revealed that eight year olds, eleven year olds, and adults used configural information for face recognition. Using a similar task, Baenninger kept facial configurations constant but manipulated features by removing them. Removing features had little negative effect on recognition for any age group. Together these experimental results indicate that both children and adults have a tendency to rely on configural cues more than featural cues during face recognition tasks. Though face processing styles appear to be similar across development, Baenninger does report age differences in performance. The author attributes age-related face recognition performance differences, in the presence of similar face processing strategies, to potential developmental differences in characteristics such as memory, motivation, attention, and experience.

Other studies suggest experience-based quantitative changes in face processing with age. In a part-whole face recognition task, Pellicano and Rhodes (2003) found that four-year old children use holistic processing for face recognition. Though their overall performance was poorer than adult performance, four and five year old children, like their adult counterparts, recognized upright faces better in the whole than in the part condition. Pellicano and Rhodes's data (2003) in accord with other data, support qualitatively similar face processing from five years to adulthood. The finding that children performed more poorly on upright face recognition than adults is in line with findings from other developmental studies (Baenninger, 1994; Diamond & Carey, 1977); and may indicate differences in levels of face expertise (Bruce et al., 2000; Diamond & Carey, 1986).

In support of expertise-based quantitative changes in the visual recognition system de Haan, Pascalis, and Johnson (2002) compared infant and adult N170 components in response to upright and inverted human and monkey face stimuli. In the study, infants did not show the same degree of cortical activation during face processing as adults. Rather, adult N170s were sensitive to species and orientation while 6 month infant responses only showed sensitivity to species. The presence of an orientation response in adults but not in infants may be linked to experience. In general, 6 month-old infants have encountered the human face many times. However, at 6 months, an infant's experience with the upright human is not as extensive as that of an adult. Thus, a sufficient amount of experience with upright faces in adults may drive the specialized N170 for inverted faces that is absent in infants. Other studies support the idea of an experience-driven N170 sensitive to inversion (Halit et al., 2000; Rossion et al., 2000).

In addition to interspecies stimuli, studies using faces of other races also demonstrate developmental changes in face processing based on experience. Some experimenters observed increasing cross-race or non-native effects with age as the observer's abilities to discriminate between two faces differing in race from his/her own race were inversely proportional to the observer's age (Chance, Turner, & Goldstein, 1982; Sangrigoli & de Schonen, 2004). Chance and colleagues examined performance in Caucasian subjects six to twenty years of age on the recognition of Caucasian and Asian faces (1982). Based on accuracy results, superior recognition for native race (Caucasian) than other race faces (Asian) appeared after seven years of age. The emergence of this non-native effect indicates faces processing changes based on exposure to stimuli. In another developmental investigation of the non-native effect, Sangrigoli and de Schonen explored the role of experience in processing inverted faces (2004). Children three to six years old and adults participated in a forced choice task where face recognition was tested according to the categories of race (Caucasian versus Asian) and orientation (upright versus inverted). Adult findings confirmed a cross-race effect and an inversion effect. The inversion effect was greater for native race faces supporting the idea that the inversion effect is related to degree of expertise with the stimuli (Diamond & Carey, 1986). For children, inversion and non-native effects increased between three to five years of age. Also, children older than 3 years showed a significant interaction of race and orientation with greater error rates for inverted native faces than inverted non-native stimuli. This development of a race x orientation interaction indicates experience-based changes in face processing. Collectively, studies using faces of other species and other races tap into changes that support an expertise basis for quantitatively different processing of faces and objects.

Summary of the “Special” Debate

Faces are and are not special. Recognizing which argument is more valid is difficult considering the amount of literature supporting each. Even for those who argue against the special status of faces, it appears that faces may be a special stimulus category based on their frequency in and relevancy to our everyday lives. Proponents and opponents of the special status of faces seem to agree that face recognition performance is to some degree experience-dependent.

Object Processing

An object’s shape is critical to its recognition. This idea comes from the discovery that neurons in cat cortex are sensitive to boundaries of dark and light and are organized in columns according to orientation preferences (Hubel & Wiesel, 1959). With this discovery, Hubel and Wiesel found that the visual system is sensitive to edges (1959). Thus, it follows that a visual system that responds to edges is ideal for recognizing object shape. Based on this idea, Marr and Nishihara proposed that visual recognition of objects functioned on an early detection system that built complex 2-D shape representations from edge information – a primal sketch (1978). Using this primal sketch, information about depth and orientation were added to form 3-D shapes.

Another well-known theory of object recognition based on shape is Biederman’s Recognition-by-Components (RBC). In contrast to holistic face recognition models, Biederman proposes that object recognition occurs by decomposition of the object into its basic parts (eg. Geons, 1987). For recognition, these parts and their spatial arrangements are then matched to structural descriptions (three dimensional compositions of an objects shape) in one’s memory (Biederman, 1987). While some investigations support Biederman’s breakdown of structural components for object processing (similar to the feature-based face recognition hypothesis) (Ward, 1989), others have shown that configural processing also occurs in object recognition (Davidoff & Roberson, 2002; de Gelder & Rouw, 2000a; Reed et al., 2003). Thus, as discussed in detail in the following section, objects, like faces, may be recognized using featural and configural processing. However, unlike face recognition, developmental changes in object recognition have not been documented.

Are Objects Special?

If faces are special, are other object classes unique? Turati et al. showed that newborns orient to general perceptual patterns of objects not specifically to face stimuli (Turati, 2004). Other evidence exists that object recognition occurs early in life. For example, infants correctly perceive an object's size despite changes in distance (size constancy) and discriminate between object stimuli (Slater, Field, & Hernandez-Reif, 2002). Furthermore, the mechanisms of 3-D object processing, object segregation, and featural relations (orientation of attributes) are available in infancy (Bertin & Bhatt, 2001; Bhatt, Bertin, & Gilbert, 1999; Bhatt & Waters, 1998). These recognition skills indicate that object processing, like face processing, emerges at birth.

Though face and object processing both exist early in human life, it has been thought that object recognition engages primarily a featural or parts-based mechanism (Carey & Diamond, 1994; Ward, 1989) while face recognition relies on relational information. One piece of evidence for featural processing of objects is the inversion effect. Unlike faces which have a pronounced inversion effect, inverted object stimuli are only somewhat more difficult to recognize than upright objects (Carey & Diamond, 1994; Yin, 1969). Because the face inversion effect is interpreted as a disruption of relational processing (Carey & Diamond, 1994; Farah, Tanaka, & Drain, 1995), the relatively small object inversion effect implies object recognition does not rely on a relational mechanism.

However, recent evidence suggests that object recognition is not limited to featural processing but, like face recognition, also involves configural processing. Some studies have found a significant inversion effect in non-face stimuli (de Gelder & Rouw, 2000b; Diamond & Carey, 1986; Gauthier & Tarr, 1997; Reed et al., 2003). In their study of prosopagnosic patient LH, de Gelder & Rouw noted similar performance on inverted faces and objects (2000a). Unlike normal adults, LH performed superiorly on inverted stimuli, faces and objects, as compared to upright stimuli (de Gelder & Rouw, 2000b). This finding was referred to as the superior inversion effect. From this finding, the authors concluded that configural information is elicited in non-face stimuli recognition as well as face stimuli recognition and that the inversion effect alone is not a sufficient test for category-specific processing (de Gelder & Rouw, 2000b). In addition to evidence from this lesion study, two studies in normal functioning healthy individuals have noted configural processing in body positions (Reed et al., 2003) and animals

(Davidoff & Roberson, 2002). In an adult behavioral study, Reed et al. investigated the effects of inversion on three classes of stimuli, faces, body positions, and houses (2003). They found that real body positions, like faces but unlike houses, produced an inversion effect. As inversion has been shown to disrupt configural processing, the authors interpreted their findings to mean that bodies, a non-face object class, may be processed configurally. As discussed previously, a greater face inversion effect in older children and adults is taken as evidence for increased configural face processing with age. Based on that idea, Davidoff & Robertson, examined the performance of children, ages 5 to 16 years, and adults on upright and inverted part and whole animal stimuli (2002). Overall, children did not reach adult levels of performance on whole stimuli and all ages performed more poorly on inverted whole animal stimuli than other stimuli x orientation conditions. The disproportional effect of development and inversion on whole animal recognition, similar to face recognition data, was interpreted as evidence for configural processing in animal recognition. Thus, existing data supports featural and configural mechanisms for faces and objects.

These findings indicate that face and object processing are potentially similar. However, face recognition also involves holistic processing (Tanaka & Farah, 1993, 2003). Thus, holistic processing may mark the qualitative difference between face and object perception. If faces are special indeed, then reason would implicate that objects would not use a holistic processing mechanism. To discern holistic from featural processing, Tanaka and Farah designed three forced-choice tasks in which participants identified face parts in the context of the whole face or in isolation. Using this same design, the authors tested three other stimulus categories as controls: scrambled faces, inverted faces, and houses. Tanaka and Farah found holistic processing was unique to upright faces compared to the other stimulus conditions (1993). Other studies also noted that holistic processing was not recruited for object recognition but limited solely to face stimuli (Moscovitch & Moscovitch, 2000; Tanaka & al., 1998). In a series of four same-different matching tasks, Tanaka et al. used selective attention and masking paradigms to discern holistic from featural mechanisms in face processing (1998). Selective attention was used to test for the featural processing of faces. Subjects made a same/different recognition judgment after being cued to focus on a particular face part. For this task, “different” face stimuli were modified by one or more face parts. In the other three experiments, masking during a same/different task was used to differentiate between holistic and featural processing of upright faces versus words, inverted faces, and houses. Masks of parts and masks of the complete stimulus were created for each condition. Tanaka and colleagues reasoned that if upright face recognition relied on holistic processing, the whole stimulus mask would produce more interference than the parts mask. In the case of featural processing, the opposite masking effect would occur. Other stimulus types were masked and tested as controls. Cumulatively, results indicated that upright faces were processed more holistically than other stimuli tested. Moscovitch and Moscovitch tested holistic versus featural face processing via a recognition task involving fractured and whole versions of upright and inverted faces (2000). In each of these experiments, holistic processing was distinguished from featural processing. In contrast, functional MRI investigations of global and local shape processing revealed evidence of holistic grouping processes for non-face objects (Grill-Spector et al., 1999; Hasson, Hendler, Bashat, & Malach, 2001; Kourtzi & Kanwisher, 2000). Thus, substantial evidence exists for holistic processing of faces but a debate remains as to whether holistic processing is employed in object recognition (McKone, Martini, & Nakayama, 2003; Tanaka & Farah, 2003).

Though objects and faces may share similar inceptions, the question remains as to whether or not objects and faces access all of the same processing mechanisms to the same degree (i.e. featural, configural, and holistic). In addition to potential differences in mechanisms, face processing may also be unique from general object processing in regards to maturation. Unlike the controversy surrounding face recognition, much research supports the conclusion that object recognition is similar in children and adults. In fact, Bower notes "it would be fair to say that, from early on in life, infants perceive these attributes (size, shape, color, identity) of objects more or less like adults" (Bower, 2002). Object recognition studies indicate similarities between adults and infants by at least 5.5 months of age in mechanisms of 3-D object processing, object segregation, and featural relations (orientation of attributes) (Bertin & Bhatt, 2001; Bhatt et al., 1999; Bhatt & Waters, 1998). Also, in a behavioral study by Ward (1989) at age five years, children demonstrated predominately analytical processing (processing which concentrates on individual attributes of an object) of non-face stimuli like their adult counterparts (c.f. de Gelder & Rouw, 2000b). Even in three and four-month old infants, performance in a perceptual categorization of cat and dog silhouettes corresponded well with adult performance (Quinn et al., 2001). In addition, infants, like adults, determined identity of objects not only at a basic level using silhouettes, but also categorized objects using similarity of surface attributes and bound contours (Quinn et al., 2001). Therefore, not only do infant and child studies support similar object recognition processing among infants, children, and adults but evidence of a similar shape processing mechanism for object recognition exists. In contrast to face recognition data, much object recognition data implies that infants, children, and adults use similar processes. Different developmental trajectories for face and general object processing may be attributed to potential differences in holistic processing.

3.) What is the Course of VPS Development?

Related to the debates concerning VPS functional organization and underlying cognitive mechanisms are the questions of VPS development. When do face and object processing develop? What inputs are necessary and what is already hard-wired? Is there a critical window of development? Is there plasticity? Can compensation occur?

As previously discussed, controversy exists as to whether the functional organization of the VPS is early determined (i.e. innate) (Farah et al., 2000; Gilchrist & Mckone, 2003; Johnson & al., 1991; Morton & Johnson, 1991) or changing and maturing with learning and experience (Carver et al., 2003; Gauthier & Nelson, 2001; Passarotti et al., 2003). Farah et al. argue for an innate face mechanism and cortical region distinct from object processing. Thus, the developmental course proposed by Farah et al. (2000) is the existence of separate, relatively unchanging, *parallel channels* devoted to the processing of different stimulus categories. Researchers supporting this domain-specific course of VPS development cite neuroimaging evidence of categorical modules for faces, places, human bodies, and letters (Downing et al., 2001; Kanwisher et al., 1997; Krieman et al., 2000; Nakamura, Kawashima et al., 2000; O' Scalaidhe, Wilson, & Goldman-Rakic, 1997; O'Craven & Kanwisher, 2000; Polk & Farah, 1998; Puce et al., 1995). In addition, lesion studies cite the lack of compensation, the function of one region or system being taken over by another, as evidence for innately specialized brain regions (Farah et al., 2000). The idea for dissociated channels of object and face recognition implies that the organization of the VPS is specified in the genome, is not altered by experience, and is not adapted in response to need.

In contrast, others support a changing and maturing VPS in which need and experience influence visual perceptual development (Turati, 2004). The idea is that children, having less sensory experience than adults, may use similar systems for *all* object processing (face and non-face stimuli). However, with age, experience with objects increases and more distinct processing may occur for sub-ordinate classifications, resulting in the development of discrete systems for more refined processing of object classes including faces. In other words, applied to the VPS, the middle fusiform gyrus can be “fine-tuned by experience with any object category” (Gauthier, Tarr et al., 1999). This experience tuning or perceptual narrowing has been proposed and supported in developmental studies of language and has some support in the realm of visual processing. In fact, recent investigations imply that face-processing skills and corresponding neural correlates narrow with development and are fine-tuned with age (Pascalis, de Haan, & Nelson, 2002; Passarotti et al., 2003). Thus, the middle fusiform gyrus may begin as a general processor in infancy with overlapping categorical processing of objects that, with exposure and experience over time, is honed into more distinct regions of processing in adulthood.

Timing is Everything: Early Development and Plasticity

In addition to the course of VPS functional and cognitive development, the general developmental course of vision is critical to face and object recognition. There is evidence of plasticity or adaptability of the brain in the primary visual cortex (V1) and visual association cortex. Though sub-regions of the lateral occipital complex in the VPS normally respond to visual and tactile information (Amedi, Jacobson, Hendler, Malach, & Zohary, 2002), studies also demonstrate auditory-derived responses in the VPS of blind individuals. For example, in congenital and early-onset blind humans, V1 activation in tactile (e.g. Braille reading) and auditory discrimination tasks indicates cross-modal plasticity of the VPS (Buchel, Price, Frackowiak, & Friston, 1998; Cohen et al., 1997; Kujala, Alho, & Naatanen, 2000; Weeks et al., 2000). In a comparison of congenitally blind subjects versus sighted subjects, Weeks et al. demonstrated a visual to auditory cross-modal plasticity. Using PET technology, the authors found responses to an auditory localization task in association areas of the right occipital cortex in the blind but not sighted individuals (Weeks et al., 2000). Similarly, using transcranial magnetic stimulation (TMS) to temporally disrupt cortical function in the occipital region, Cohen et al. found distorted tactile perceptions in early blind subjects but no effects on controls (1997). Hence, visual regions of the cortex display some plasticity.

The mechanisms of plasticity are shown to differ depending on the time frame of the disorder. In a PET study of Braille reading and auditory word processing, activation occurred for both tasks in the visual cortex of blind subjects whether their deficit was congenital or followed puberty (Buchel et al., 1998). This study indicates that plasticity changes may occur even after childhood. In other cross-modal plasticity studies, early-onset (prior to 5 years) blind individuals showed evidence of occipital activation to tactile stimuli equivalent to visually-produced activation in non-blind controls whereas late-onset (later than twelve years) blind subjects had no VPS activation relative to the other two subject groups (Chen, Cohen, & Hallett, 2002; Cohen et al., 1999). Findings of restricted cortical function in late onset blindness indicate a critical period of plasticity in which the developing brain is more capable of acquiring a specific ability than the adult brain. Based on the studies above, the critical period for optimal cross-modal plasticity in the VPS appears to be younger than five years old. These studies, though cross-modal, demonstrate the existence of a critical period of functional plasticity for the VPS.

However, findings from deficits in visual acuity and perception indicate less intra-modal plasticity and a much earlier window of opportunity for optimal development. In a fMRI study of adult amblyopic subjects versus controls, Lerner and colleagues investigated the effects of early visual deprivation on the visual system (2003). Amblyopia, a developmental visual disorder occurring in early childhood, is characterized by reduced acuity and sensitivity contrast in one eye. For separate stimulation of each eye, participants wore red-green glasses to view red and green colored pictures of famous and unfamiliar faces and buildings. In the magnet, subjects performed a one-back memory task and a recognition/categorization task. The activation maps corresponding to the affected eye in the amblyopic subjects revealed significantly reduced activation in face-related regions of visual association cortex relative to controls. In contrast, in amblyopics, no significant reduction of activation occurred in building-related areas for either eye. These face-specific deficits were not present in primary visual cortex. Lerner et al. concluded that early visual input is critical to the normal development of higher-order visual regions, particularly face processing areas. In another study, patients treated for congenital bilateral cataracts had severe impairments in configural but not featural face processing (Le Grand, Mondloch, Maurer, & Brent, 2001). Similar to the amblyopic study results (Lerner et al., 2003), this study cites the importance of early visual experiences to the normal development of face processing but further identifies the deficit as configural. Also, in a behavioral study, Mondloch et al. (2003) determined that early visual experience (birth to 2 months) was necessary for the development of normal holistic processing and sensitivity to second-order relations but not for face detection and first-order processing.

The importance of early visual experience for the development of normal cortical processing in humans is in agreement with Hubel and Wiesel's well-known visual deprivation studies in cats (1959). Using single cell recordings, Hubel and Wiesel found normal distribution of ocular dominance cells in primary visual cortex. To discern the effect of visual experience on visual cortex development, Hubel and Wiesel closed one eye of the cat early in life and allowed the cat to mature to adulthood. Electrophysiological recordings revealed very few cells were driven by stimuli presented to the reopened eye. Thus, the deprived eye was functionally disconnected from the visual cortex. Furthermore, the effect was permanent. Hubel and Wiesel found little to no recovery. In addition, no functional cellular changes were evident when the same experiment was performed on an adult cat. Hence, Hubel and Wiesel concluded that there is a critical period of development in which visual experience determines how visual cortex is wired (Purves et al., 2001).

From these and other studies (Bentin, Deouell et al., 1999a; Gregory, 2003; Innocenti, Kiper, Knyazeva, & Deonna, 1999) normal visual development in childhood appears to play a vital role in VPS development. However, the specific role remains unclear. Though many of these studies imply visual input between birth and 6 months of age is most critical to the development of face processing, evidence further indicated a specific break-down in the development of relational processing. As maturation of face recognition is slow (Mondloch et al., 2003) and face recognition occurs at the subordinate level (Tarr, 2003) adverse effects of early visual deprivations on relational processing may reflect deficits in expertise-based recognition rather than categorical-based recognition. Thus, as evidenced by the effects of early visual deprivation, plasticity of the VPS for visual recognition is limited. Understanding the normal course of VPS development and the potential for plasticity may provide the basis for therapeutic (Innocenti et al., 1999) and pharmacological intervention for prevention and treatment of disorders involving face and object processing deficits.

III. Current Research Focus

The existing debates and gaps in the literature concerning development, functional organization, and underlying cognitive processing of face and object recognition in school-aged children serve as the driving force behind this research project. To date, visual recognition and the ventral processing stream have been studied extensively in human adults but pediatric neuroimaging data are just recently being gathered. Though face and object recognition have been well-researched, the developmental courses of these recognition processes during early, middle, and late childhood have received relatively little attention (Want et al., 2003).

Thus, this research project focuses on the development of the functional organization and underlying cognitive mechanisms of face and object recognition in children five to eleven years of age. Age ranges for the child groups corresponded to ages investigated in published behavioral face and object studies (Carey & Diamond, 1994; Schwarzer, 2000; Ward, 1989). Using neuroimaging and behavioral methods of investigation, I address three major questions:

1. What are the neural correlates for face and object recognition in children?
   in adults? (Chapter 4)
2. By what mechanism(s) are faces and objects processed? (Chapter 5)
3. What developmental changes occur? (Chapters 4-6)

Though changes from five to eleven years may not be as distinct, and arguably not as critical as brain development at younger ages, the more discrete differences in these age groups reflect fine-tuning of visual processing that are nevertheless important in the maturation of the visual recognition system.

The establishment of normative data on the development of the ventral processing stream and corresponding cognitive processes is important in understanding the neurobiology of both normal and abnormal visual processing. So that, in the words of autistic authorTemple Grandin (Grandin, 1995):

"... as more educators and doctors understand these differences, more children with autism (and other visual processing deficits) will be helped ... at younger ages."

Chapter Two: Project Overview and Preliminary Experiments

In the current project, functional MRI and behavioral methods were used to determine the neural correlates and corresponding cognitive mechanisms involved in the typical development of face and object recognition. Functional MRI, a relatively recent neuroimaging method, provides structural anatomical correlates of neural behavior. Using fMRI, researchers simultaneously record patterns of brain activity and behavioral responses associated with particular cognitive tasks. The link between brain activity and behavioral responses provides a map of mental processes. Thus, in the present work, fMRI provides a means of mapping developmental changes in brain functions associated with the maturation of cognitive functions.

In regards to other functional neuroimaging techniques, fMRI offers two distinct advantages. Unlike its forerunner, positron emission tomography (PET), fMRI is non-invasive. PET relies on the injection of radioactive tracers to measure metabolic changes in glucose associated with brain function whereas fMRI uses an endogenous contrast agent, natural changes in blood oxygenation levels over time, to identify brain activity. In the brain, blood oxygen levels change in response to neuronal activity. As neuronal activity increases there is an increase in the ratio of oxygenated to deoxygenated blood. Deoxygenated blood is highly paramagnetic. As neural activity increases in a region, the surplus of oxygenated blood interferes with the paramagnetic properties of unbound hemoglobin in deoxygenated blood resulting in an increased MR signal. This blood-oxygenation-level dependent effect (BOLD) serves as the basis for fMRI. Therefore, because it provides a non-invasive method for localizing brain activity, fMRI is the method of choice for our developmental study of healthy children and adults.

A second advantage of fMRI over other modes of neuroimaging is its good spatial resolution. In addition to PET, electroencephalography (EEG) and magnetoencepalography (MEG) are used to evaluate brain function. EEG and MEG, methods of measuring rapidly changing electromagnetic properties of brain activity by placing devices outside the skull, are less invasive than PET. These electromagnetic techniques are valuable for determining the timing of brain processes but provide poor spatial information (Huettel & Song, 2004). Because we wanted to identify unique maturational changes in the neural correlates of face and object processing, we chose to use fMRI in this study for its superior spatial resolution. Overall, fMRI provided us with a non-invasive method for mapping spatial changes in brain activity as a function of development in normal, healthy subjects.

Preliminary Studies

Three previous adult visual recognition studies (Preliminary Studies 1-3) serve as the foundation for the current experiments. Overall, findings from these adult studies challenged the idea of domain-specificity in the VPS and introduced a new impetus for VPS architecture. Faces, objects, and letters produced differential not selective responses to categories in the adult VPS (Joseph & Gathers, 2002; Joseph, Piper, & Gathers, 2003) pointing to a distributed rather than modular VPS architecture.

These results implied that taxonomic category failed to explain the basis for the VPS functional blueprint. Instead, another idea was proposed – a structural similarity mechanism. Structural similarity refers to the degree of structural overlap (i.e. shape overlap) between competing stimuli. In other words, a structural similarity mechanism implies that VPS neural substrates are sensitive to variations in object structure rather than taxonomy. The structural basis of VPS organization was tested using fMRI tasks manipulating structural overlap in pairs of animal and shape stimuli (Joseph & Gathers, 2003). The details of these preliminary investigations are discussed here.

Preliminary Study 1: Face and Object Localizer

In this fMRI study, we questioned the existence of a VPS module responsive solely to face stimuli (Joseph & Gathers, 2002). A conservative hypothesis testing approach (Joseph et al., 2002) was used to determine if VPS regions responded in selective, graded, or conjoined fashions. A selective response would involve significant activation by one stimulus category relative to fixation and other stimulus categories and responses to all other stimulus categories would not be significantly greater than fixation. In other words, regions showing a selective response would be activated exclusively by the category of interest. Graded activation refers to statistically greater activation by one category than one or more others but at least two categories produce a response statistically greater than that of fixation. For example, a face-graded region would respond to faces significantly more than to other objects and baseline but also other objects would produce a statistically significant response in the region relative to baseline. For a conjoined response, two or more stimulus categories produce significant activation in a region relative to fixation yet statistically equivalent to one another. Thus, conjoined regions would produce statistically equivalent responses to potentially multiple stimulus types.

Participants

Thirteen normal, healthy adult volunteers (five males, mean age 20.8 years, 8 right-handed) with normal or corrected-to-normal vision were compensated for their participation. Data from four subjects were omitted from further analyses due to excessive head motion.

Design and Procedure

In the MRI scanner, adults passively viewed gray-scale photos of natural objects (N), manufactured objects (M), and unfamiliar faces (F). This nine-minute face and object localizer task (Joseph & Gathers, 2002) consisted of nine pseudorandomized task blocks, 3 for each category (F, M, N), interleaved with eight fixation blocks (17.8 sec each). Each block consisted of 30 randomly ordered stimuli presented for 1000ms each and followed by a fixation crosshair for 400ms. See Figure 2.1. To encourage attention to the task, subjects were instructed to press the button under their right index finger each time a picture appeared but not to respond to fixation. We analyzed the data collected using the logical combination approach (Joseph et al., 2002) to identify selective, graded, and conjoined brain patterns as defined above. Details of the approach are outlined in Chapter Three and Appendix A.

Results and Discussion

Brain activation patterns revealed an extensive conjoined response in the fusiform gyrus for faces and objects relative to visual fixation. No selective responses occurred for any single stimulus category. Shared (co-localized) rather than dissociated neural substrates implied no module existed in the adult VPS exclusive to face processing. Thus, we did not find support for categorically-driven neural organization of the VPS. In Chapter 4 of the current project, the same passive localizer task was used to investigate the degree of category selectivity in the VPS of children. The main goal of Chapter 4 was to identify developmental changes in the VPS neural correlates of face and object processing from 5 years to adulthood.

Preliminary Study 2: Object and Letter Processing

Some investigators support a domain-specific functional organization of the human cortex. Previous studies imply that different stimulus categories such as faces (Kanwisher et al., 1997), body parts (Downing et al., 2001), and letters (Gros et al., 2001; Polk et al., 2002), or word forms (Leff et al., 2001; Petersen et al., 1990) recruit category-specialized regions of the cortex during visual processing. In contrast, we hypothesized a domain-general organization in cortical regions responsible for visual processing. As in the previous studies, we used objects and letters, as well as visual noise for a control condition, to examine the extent of similar and dissociated neural resources recruited for recognition (Joseph et al., 2003). We proposed that object and letter recognition would recruit similar neural regions to an equal degree.

Participants

Thirteen right-handed, English speaking adults (8 females, mean age 26.4 years) participated in the fMRI experiments. All subjects had normal color vision and normal or corrected-to-normal visual acuity. No histories of psychological or neurological illnesses were reported. Two sets of data were omitted due to anatomical abnormalities in one subject and reports of letter reversal by another subject.

Design and Procedure

Twenty-six upper and lower case versions of letters from the English alphabet were used for letter stimuli. Fifty-one line drawings of animals were used for object stimuli. Visual noise stimuli were derived from pixilated forms of the letters and objects. An asterisk served as visual fixation.

Each subject participated in three experimental runs. Each run consisted of nine task blocks (42 sec) interspersed with nine fixation blocks (block 1 = 12.7, 2-8 = 18.7 sec). For each run, three task blocks occurred in pseudorandom order for each of the three stimulus types (objects, letters, noise). Each task block contained 21 randomly ordered stimulus trials. Each trial was presented for 200 ms followed by a fixation for 1800 ms. For runs 1 and 2, subjects passively viewed the stimuli. In run 3, participants were instructed to silently name objects and letters and ascribe the name “blob” to visual stimuli.

FMRI data was analyzed with MEDx software (Sensor Systems, Sterling VA). The logical combination approach (Joseph et al., 2002) was used to identify selective, graded, and conjoined regions of activation for each of the four stimulus conditions: letters, objects, noise, and fixation.

Results and Discussion

Conjoined activation of letters and objects, co-localized and statistically equivalent in magnitude, occurred in the left fusiform and inferior frontal gyri while letter-selective responses, exclusive to letters, presented in the left inferior parietal lobule and left insula. Though letter and object processing are not completely shared considering the presence of selective activity in the left inferior parietal lobule, the presence of conjoined rather than selective activation in the left fusiform gyrus argues for some similar cognitive basis in letter and object processing and against category-specific modules in the VPS. Similar to Preliminary Study 2, the current work explores the extent of shared and dissociated neural correlates for objects (manufactured and natural) and faces in the VPS (Chapter 4) and in other cortical regions (Chapter 6) from childhood to adulthood.

Preliminary Study 3: Structural Similarity Mechanism

The goal of this study was to determine if fMRI responses in the fusiform gyrus were driven by differences in shape or structural similarity (SS) among objects rather than by strict category distinctions (Joseph & Gathers, 2003). Structural similarity was based on the similarity or overlap of structural descriptions. Structural descriptions are abstract representations of the components of objects specified by sizes of the components as well as spatial arrangement of the components (Biederman, 1987). In a same/different perceptual matching task, we parametrically varied degrees of SS between two objects within the same category. If structural processing is a principle organizing factor in the fusiform gyrus, we predicted fMRI signal in this region would be modulated by our manipulations of SS. In particular, we hypothesized that more anterior regions of the fusiform would be responsive to high SS processing while relatively more posterior regions would be sensitive to low SS processing.

Participants

In Experiment 1, twelve healthy, right-handed adults were scanned. Two were omitted for motion and image artifacts. The remaining ten consisted of 5 males and 5 females (mean age 28 years). In Experiment 2, five subjects were omitted from the original 16 scanned due to motion and image artifacts. Data from eleven healthy adults (5 females, mean age 24 years, 9 right-handed) were submitted to further analyses. For both experiments, subjects had normal or corrected-to-normal vision and no histories of psychological or neurological illnesses.

Design and Procedure

In **Experiment 1**, subjects completed two functional runs of an animal matching task. Line drawings of animals from several different classes served as stimuli. Pairs of animal stimuli were assigned to one of four SS levels (12 pairs per level) based on a previous rating study (Joseph, 1997) with SS1 representing little overlap in the animals' structures and SS4 representing a great degree of structural overlap. Subjects were asked to discern if the two stimuli in each pair were the same animal. Matching pairs were "same" animal pairs varying only in orientation while non-matching pairs were "different" animal pairs parametrically varied across the four similarity levels. Stimulus pairs low in SS consisted of animals having very different body shapes such as 'toad versus dolphin'. In contrast, high SS pairs included animals with similar body shapes and features. For example, at high SS levels subjects viewed the stimulus pair 'dog versus horse' in which both animals had elongated, cylindrical bodies, four legs, visible ears, and tails. See Figure 2.2a. Behavioral and fMRI signal change responses were recorded.

In **Experiment 2**, subjects completed three experimental runs: animal matching, shape matching, and a passive-viewing face and object localizer task. The animal matching was the same as in Experiment 1 and the localizer task is described above (Preliminary Experiment 1). The shape stimuli were twelve line drawings of 3-D shapes from a previously published report (Biederman, 1987) in which the shapes were classified along four dimensions including: curved or straight edge of the cross-section, rotational or rotational and reflectional symmetry of the cross-section, constant or expanded size of the cross-section along the longitudinal axis, and straight or curved longitudinal axis of the shape. Shape pairs were assigned to one of three SS levels (10 pairs each) as determined by the number of dimensions in which the two shapes overlapped. See Figure 2.2b.

For the matching tasks, subjects were asked to discern if the two stimuli in each pair were the same animal or shape. In the animal matching task, matching pairs were “same” pairs varying in exemplar and left/right orientation while non-matching pairs were “different” pairs parametrically varied across the similarity levels and potentially differing in left/right orientation. For the shape matching task, matching pairs were the “same” exemplars varying only in orientation whereas non-matching pairs were “different” stimuli parametrically varied across similarity levels and orientation. Subjects were taught to press a button under their index finger for “same” responses and under their middle finger for “different” responses. Stimuli appeared simultaneously as one picture above a fixation point and one below. Each pair appeared for 400 msec followed by a 1600 msec fixation.

Results and Discussion

For the behavioral results of both animal and shape stimuli, response times and error rates increased as SS increased (Figure 2.3). Post-test naming revealed animals (mean name agreement, M = 85.2 % , SD = 15.9 %) but not shapes (M = 35.6 %, SD = 22.3 %) were meaningful and nameable. Thus, these behavioral results implied a structural similarity effect existed for objects regardless of semantic content. For fMRI responses, left midfusiform regions were responsive to high SS in animal and shape tasks. Low SS activation common to both stimulus types occurred in the right lingual gyrus. Overall, fMRI signal changes indicated a pattern of greater sensitivity to high SS in anterior-mid fusiform regions and greater sensitivity to low SS in posterior VPS regions (Figure 2.4). Behavioral and fMRI responses suggested the possibility of a structurally sensitive object processing mechanism. Because fMRI responses in the fusiform gyrus were driven by different demands on processing object structure, category distinctions may not be the only organizing principle for the fusiform gyrus. These results argue against categorical specialization within the fusiform gyrus in adults. Instead, these studies suggest that mid-fusiform areas are activated by categories other than faces and that the fMRI response in these regions is modulated by structural object processing. This evidence served to motivate the experiments in Chapter 5 which examine the relationship between structural processing and fMRI responses in the child's brain.

Pediatric Pilot Studies

Building on these adult studies, the current experiments in Chapters 4 through 6 explore VPS functional architecture and the possibility of a structural-based visual recognition mechanism in children. However, prior to the current experiments, two pilot studies, one behavioral and one functional MRI, were conducted to address concerns about performance and feasibility.

Pilot Study 1: Pediatric Behavioral Responses

Prior to the current developmental experiments, a behavioral study provided information regarding optimal design for different age levels in regards to accuracy, reaction time, and emotional responses.

Participants

Fifteen normal, healthy children (5 -11 years) and 15 normal, healthy adults participated in the behavioral tasks. Subjects had normal color vision and normal or corrected-to-normal visual acuity. As a measure of cognitive function, receptive and expressive language skills were tested and found to be within normal limits for 12 children and all adults (i.e. age equivalent norm was equal to or greater than -1 standard deviation of the chronological age).

Design and Procedure

Subjects performed multiple runs of face-matching and animal-matching tasks using a serial response box attached to a Dell Computer running E-prime 1.0, Beta 5.0 (Psychology Software Tools, Pittsburgh, PA). These tasks were 5 minute versions of those described in Preliminary Experiment 3 with a few design exceptions. Stimuli were pairs of animals and pairs of faces. Structural similarity (SS), the degree of three dimensional shape overlap between stimuli, served as the independent variable while reaction time (RT) and error rates served as dependent measures. Pairs of animals and faces were assigned to one of three SS levels. To equate for performance across age groups, exposure duration of stimuli was manipulated across blocks. We identified optimal stimulus presentation time for both children and adults to perform with acceptable accuracy (greater than chance) and minimal anxiety on task (Bookheimer, 2000; Casey, Giedd, & Thomas, 2000). Stimuli were presented for 500ms, 1000ms, 1500 ms, 2000ms or 2500ms per task block. The fixation time varied in accordance with stimuli presentation time for a total response time of 3000ms per trial. Adults and children were divided into subgroups and each subgroup performed 3 blocks of each task with stimuli presentation rates of 500, 1000, and 1500ms or 1500, 2000, and 2500ms.

Results and Discussion

Adults commented on the rapidity of stimulus presentation rate at 500ms but completed the task with 88% accuracy whereas, at 500ms and 1000ms, children's performance measures were 64% and 71% accuracy respectively. In addition, the 500ms and 1000ms rates caused emotional distress in some children too anxious to complete the tasks. After testing at all six presentation rates, 2500ms was found to be the optimal stimulus duration to accommodate children (81% accuracy) and adults (94% accuracy).

In addition to equating for accuracy across age groups, we evaluated age differences regarding the performance measure of RT. In Figure 2.5, we collapsed reaction time and error data across durations. Despite a general tendency for significant differences in reaction time and error rates, overlap in performance did occur between some children (n=11) and adults (n=15). (Data from 1 child was excluded due to poor behavior and 3 others were excluded based on screening test scores & /or near-chance performance on tasks.) Thus, this preliminary study provided information supporting the feasibility of equating task performance (error and RT) across ages.

This study also provided information concerning structural processing across categories. In Figure 2.6, where data is collapsed across durations, log reaction time is depicted as a function of SS for matched ("same") pairs and unmatched ("different") pairs. As parametric manipulation occurred only within "different" pairs, assessment of same/different functions verified the use of SS processing. The functions for "different" pairs indicated similar processing for animal and face stimuli in adults but differences in categorical processing in children. In adults, reaction times for "different" face and animal stimuli pairs followed a pattern of increasing RT with increasing SS. However, in children, reaction times for “different” face stimulus pairs did not reflect SS processing, as RT did not systematically increase with increasing SS. Therefore, face processing in adults but not in children was based on a structural similarity mechanism.

Pilot Study 2: Pediatric Functional Study

In addition to the behavioral pilot study, a functional pilot study provided evidence of project feasibility and potential developmental changes in the neural correlates of face and object processing (Gathers & Joseph, 2003b).

Participants

Seven normal, healthy children volunteers ages 5-11years (3 males, 4 females, mean age 8 years) participated in the current study. All children completed the experiments. No emotional distress was reported. Data from one subject was omitted due to excessive motion artifact.

Design and Procedure

In the scanner, subjects completed three experimental runs: (1) a face and object localizer task run and two runs of a shape-matching task (similar to shape-matching task in Preliminary Study 2b). We only report results from the localizer task. The localizer task design and procedures were the same as the adult localizer design and procedures in Preliminary Study 1. As in Preliminary Study1, face localizer data were analyzed using the logical combination approach (Joseph et al., 2002) to identify selective, graded, and conjoined activation patterns.

Results and Discussion

A group analysis was performed on the imaging data. Following data preprocessing, paired t-tests of mean conditions were used to establish contrasts for face-preferential, face-selective, face-object-graded, and face-object-conjoined statistical maps. Overlays of face-preferential (blue), face-object graded (yellow), face-object conjoined (red) are seen in the images in Figure 2.7a. Though extensive face-object conjoined activation occurred in the VPS it should be noted that this group analysis involved a small sample size including multiple age levels of children. Results of this pediatric pilot analysis were compared to our adult studies (Preliminary Study 1). See Figure 2.7b. In both children and adults, most of the responses in the fusiform gyrus were explained by a conjoined activation for faces, natural objects and manufactured objects. Face preferential areas in children were almost completely explained by a graded response to faces and objects. In adult fusiform regions, face preferential activation overlapped with face-graded responses but not with face-selective responses. Thus, in children and adults much of the face responsive fusiform regions were involved in processing information associated with many different visual categories.

In general, VPS organization appeared similar for school-aged children and adults. However, developmental differences in activation patterns did occur. Minimal face-selective regions emerged in both children and adults. These face-selective regions were different in the two age groups – in children, a face-selective area emerged in the left posterior fusiform and in adults, face-selective regions emerged in the left insula, left hippocampal region, the left cerebellum, and the right inferior frontal gyrus. Though these findings did not exclude the possibility of a face module and domain-specificity, they support developmental changes in face processing and the neural correlates associated with faces. Furthermore, no manufactured- or natural-selective regions of activation occurred in children as compared with adults (manufacture-selective activation occurred in the right calcarine sulcus and right middle occipital and natural-selective activation occurred in the left temporal pole). These maturational differences in category-selective activation support potential developmental changes in the neural correlates and of visual processing from childhood to adulthood. Thus, child performance and imaging results from our functional pilot study support the feasibility and relevance of the current developmental project.

Collectively, these preliminary adult studies and pilot pediatric studies serve to motivate the present set of experiments. The following chapters will extend the ideas and results discussed in this chapter to determine the typical neural and cognitive features of face and object recognition in children five to eleven years of age and to ascertain developmental changes from childhood to adulthood. In particular, Chapter 4 will focus on the VPS organization in children and adults for face and object recognition processing. Chapter 5 will explore the idea of a structural similarity processing mechanism for objects and faces across development. Finally, Chapter 6 will go beyond findings in the VPS to include maturational changes in neural correlates for face and object processing throughout the brain.

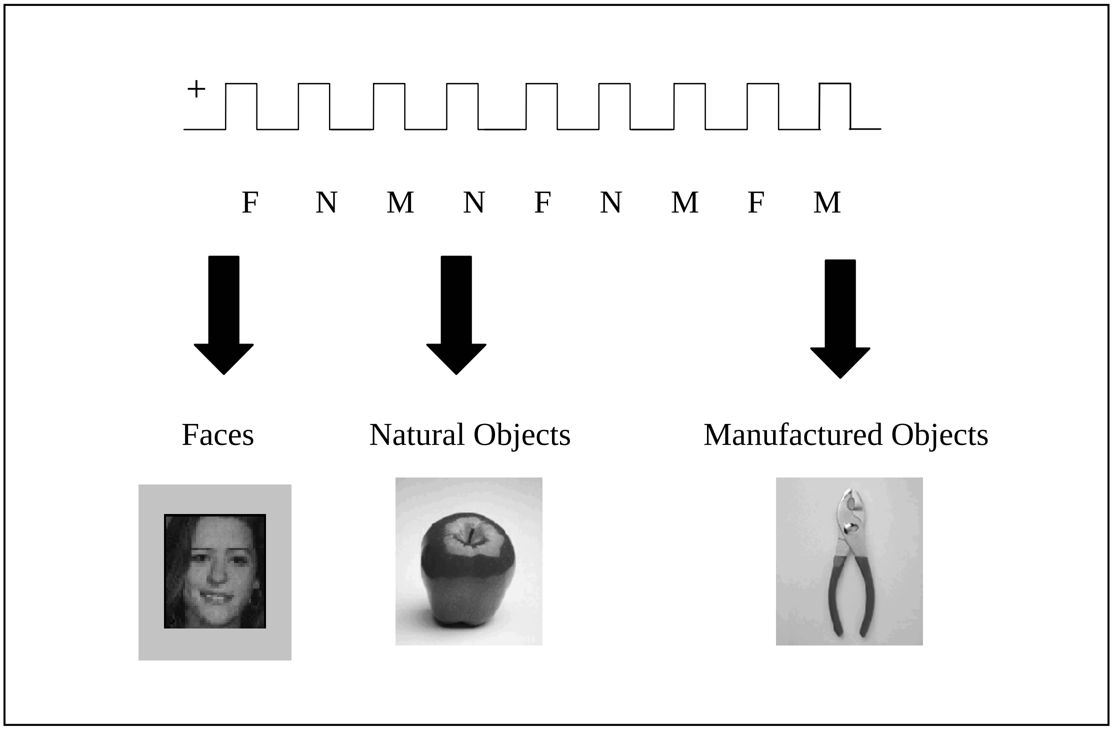
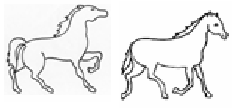
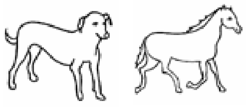


Figure 2.1 Face Localizer Task & Sample Stimuli

(A)

Structural Similarity Level	“Same” trials	“Different” trials	Structural Similarity Rating
SS1			**183**
SS2			**422**
SS3			**539**
SS4			**736**

(B)

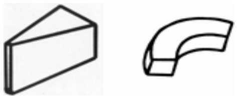
Structural Similarity Level	“Same” trials	“Different” trials	# of Shared Dimensions
SS1			**1**
SS2			**2**
SS3			**3**

Figure 2.2. Example stimuli for animal and 3-D shape matching tasks. (A) Sample animal pairs for each of the four levels of structural similarity (SS1-SS4). Mean SS ratings for “different” trials in last column. (B) Sample 3-D shape pairs for each of the three SS levels (SS1-SS3) with SS criteria for different pairs in final column.

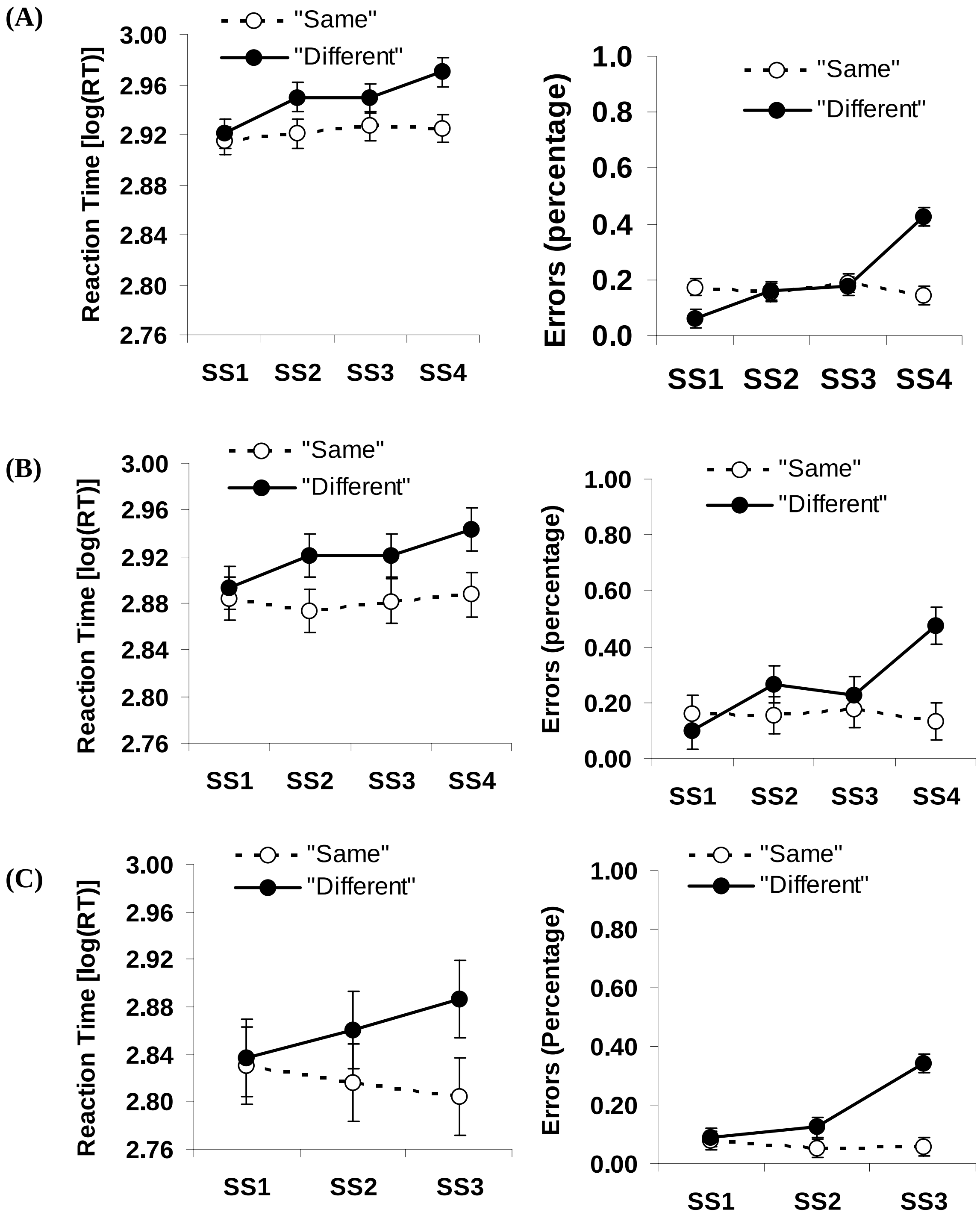


Figure 2.3. Preliminary Study 3. Behavioral measures of structural similarity (SS). Adult RT's and Err's as a function of SS for "same" and "different" trials. (A) Experiment 1, Animal-Matching Task (B) Experiment 2a, Animal-Matching Task (C) Experiment 2b, Shape-Matching Task. Error bars reflect within-group confidence intervals. Copyright 2003 Psychonomic Society, Inc.

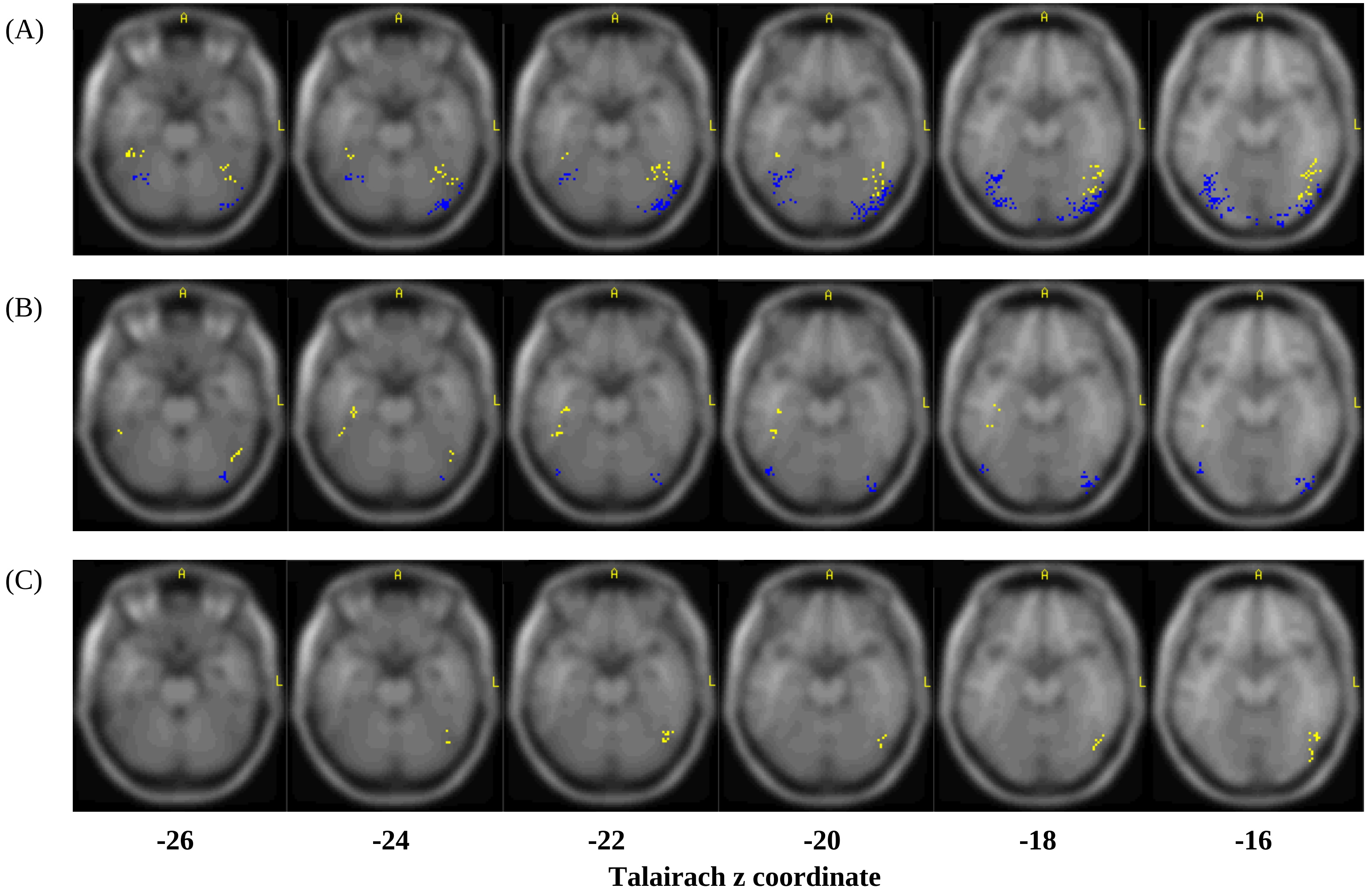


Figure 2.4. Preliminary Study 3. Functional results of group-averaged OT regions (-26 to -16mm inferior to a plane through the anterior and posterior commissures) modulated by structural similarity (SS). Animal-Matching Task (A) Experiment 1 and (B) Experiment 2 and Shape-Matching Task (C) Experiment 2. Yellow voxels represent significant increases in fMRI signal with increasing SS levels and blue voxels represent a signal increase with decreasing SS levels.
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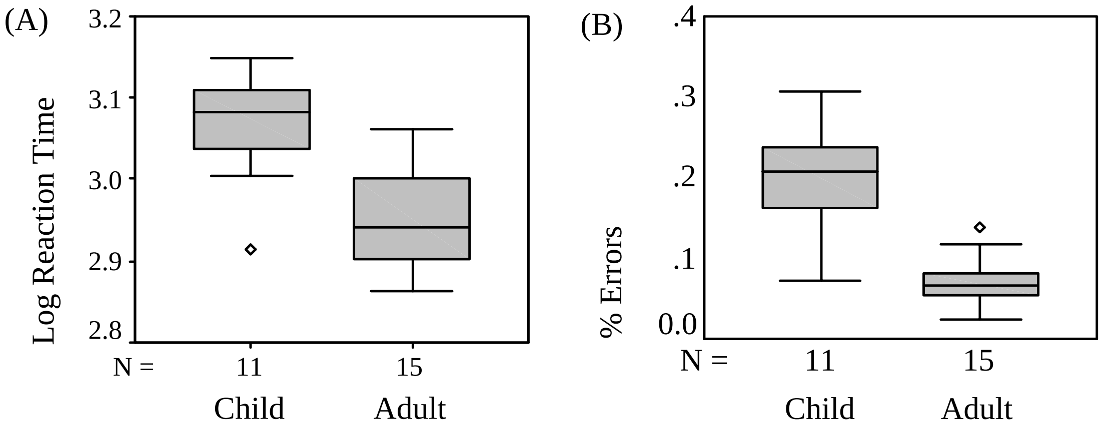


Figure 2.5. Pilot Study 1. Boxplots of performance overlaps in (A) reaction times (RTs) and (B) error rates (Err) of child and adult groups. Average log RT and percentage errors collapsed across all stimulus presentation durations.

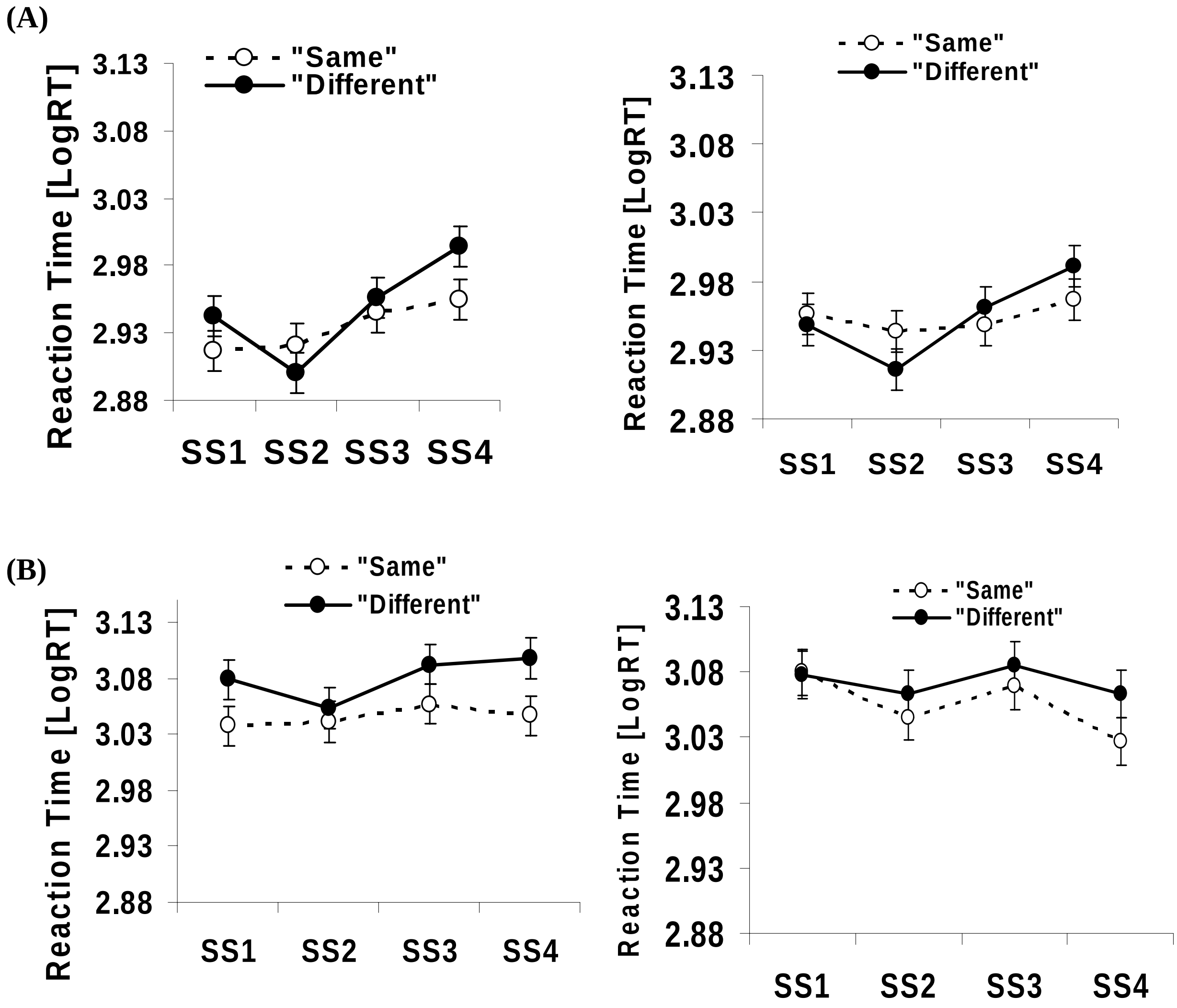


Figure 2.6. Pilot Study 1. Reaction times (RTs) as a function of SS for “same” and “different” trials. (A) Adult RTs averaged across durations for animals (left) and faces (right). (B) Child RTs averaged across durations for animals (left) and faces (right). Error bars reflect within group confidence intervals.

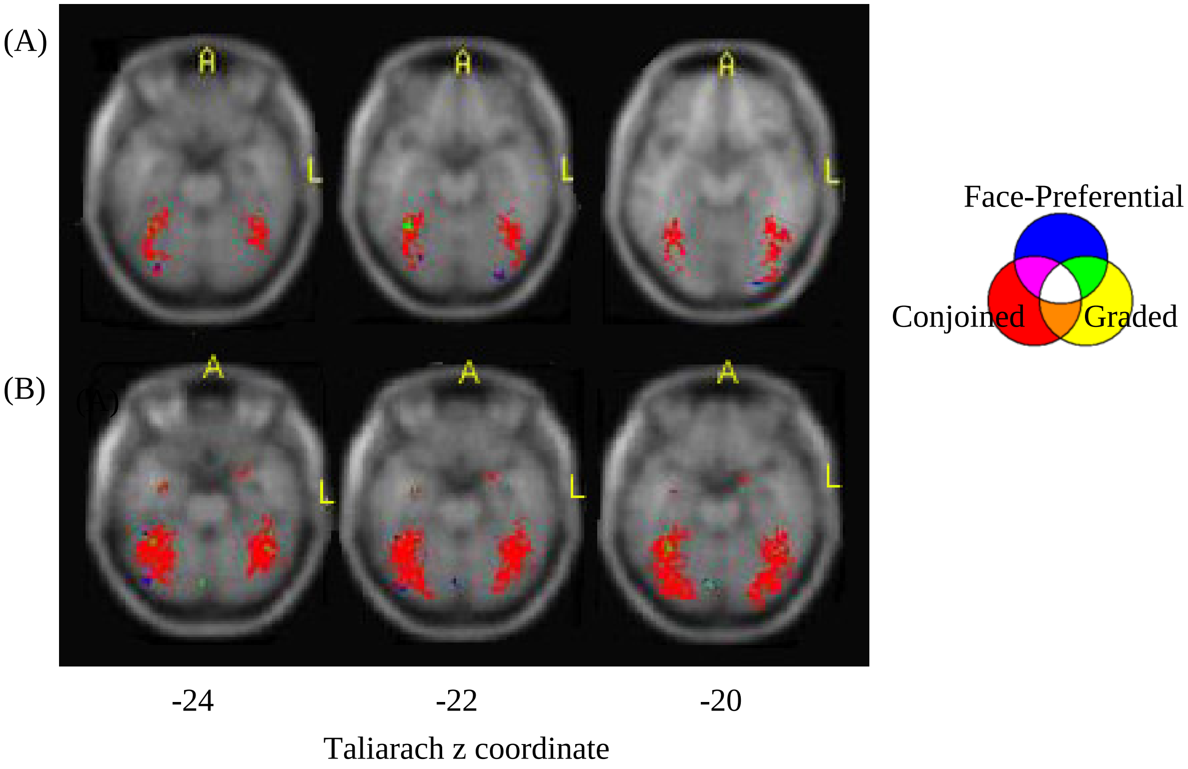


Figure 2.7. Face localizer task group analysis. Using the logical combination approach (Joseph, Partin, and Jones, 2002), we isolated face-preferential activation (blue), face-object graded activation (yellow), and face-object conjoined activation (red). (A) Pediatric group map represents multiple age levels. n = 6 (mean age 8 years). (B) Adult group map from Preliminary Study 1 for comparison. n = 13. Taliarach z coordinates of -24 to -20 mm inferior to a plane through the anterior and posterior commissures.

Chapter Three: Materials and Methods

In this chapter, we discuss the details of the materials and methods used for the experiments in Chapters Four through Six. Experimental designs and stimuli are described as well as behavioral and functional MRI analyses. Initial screening and testing procedures were performed on all participants. All three experimental chapters (4-6) involve the passive-viewing face localizer task. In addition, Chapter 5 includes a same/different shape-matching task.

Initial Screening and Testing

Prior to participation in the project, potential subjects were screened for eligibility. Exclusion criteria included adverse health conditions and factors affecting normal cognitive functioning on the required tasks. Upon arrival at the lab, eligible subjects underwent further screenings and testing. Visual acuity was tested using the Snellen eye chart. Subjects also participated in color vision (HRR color plates) and handedness (an adaptation of the Edinburgh Handedness Survey) testing. Using the Peabody Picture Vocabulary Test (Dunn & Dunn, 1997) and the Expressive Vocabulary Test (Williams, 1997), we assessed receptive and expressive language skills respectively as a measure of general cognition. Children gave written assent and parents provided written consent in accordance with the guidelines of the University of Kentucky Institutional Review Board. Adults gave written consent prior to participation.

Face Localizer Task Design and Procedure

Subjects completed a 9-minute run consisting of eight fixation (fix) blocks interleaved with nine, 42-second, pseudo-randomly ordered task epochs: 3 each of human faces (F), natural objects (N, fruits and vegetables), and manufactured objects (M, tools and everyday objects). Within each task block, 30 randomly-ordered stimuli appeared for 1000 msec each followed by a fixation cross for 400 msec. Sixty grayscale photographs scanned from a high school yearbook served as face stimuli. Grayscale photographs of 30 natural and 30 manufactured objects were obtained from Photodisc CD (Photodisc, Seattle, WA) or scanned from The MacMillan Visual Dictionary (Corbeil & Archambault, 1992). During task blocks, participants viewed the face and object pictures and pushed a button each time a picture appeared. During fixation blocks, volunteers fixated a single crosshair presented for 18 seconds (baseline). (See Figure 2.1)

Pictures were projected onto a screen using an LCD projector connected to a Dell Computer running E-prime 1.0 (Psychology Software, Pittsburg, PA) and participants viewed the stimuli (visual angle of 6.74 degrees) via a mirror on the head coil. Computerized training preceded the experiment to ensure subjects could perform the task.

fMRI Data Acquisition and Preprocessing

A Siemens Vision 1.5 T magnet equipped with a head coil and a T2*-weighted gradient echo sequence was used for functional image collection (40 ms echo time, 64 x 64 matrix, 230 mm field of view, 46 3-mm slices with a 20% gap acquired in ascending order, 6s repetition time). These parameters allowed whole brain coverage with 3.6 mm^3 voxels. For the face localizer task, seven volumes were collected per task epoch and three volumes per fixation epoch. In the shape-matching task, eight time points were collected per task epoch and two time points per fixation epoch.

Medx software (Sensor Systems, Sterling, VA) was used for all functional imaging analyses. For the face localizer task, after the first three fixation volumes of each participant's time series were discarded, the remaining 87 functional images were motion corrected using automated image registration (AIR). For the shape-matching task, the first two fixation volumes were discarded and the remaining 88 were submitted to motion correction. In Chapters Four and Six, functional runs were discarded when the center of intensity of a volume was not corrected to within .2 mm of the first time point. Using root mean squared error (RMSE) as a measure of head motion, repeated-measures ANOVAs indicated significant interactions of head motion (before and after correction) and age (children v. adults): children had more motion before correction than adults for anterior-posterior [$F(1,27) = 5.2$, $p<.031$] and superior-inferior [$F(1,27) = 5.3$, $p<.03$] planes, but these differences did not persist after motion correction. For our data analyses in Chapter 5, functional runs were discarded when the center of intensity of a volume was not corrected to within .4 mm of the first time point. Using root mean squared error (RMSE) as a measure of head motion, repeated-measures ANOVAs indicated significant interactions of head motion (before and after correction) and age (children v. adults) in the superior-inferior plane [$F(2, 30) = 7.9$, $p<.002$]: children had more superior-inferior motion before correction than adults [$F(1,31) =8.9$, $p<.006$] but age differences in head motion did not persist after motion correction [$F(1,31) = .015$, $p<.904$].

Three-dimensional spatial filtering was applied to the motion corrected time series (Gaussian FWHM = 6 mm^3; kernel size 9 pixels) and the images underwent global intensity normalization to scale the voxel intensities to a mean of 1,000. High pass filtering was applied to the data (Butterworth filter period =120s). As in other developmental fMRI studies (Kang, Burgund, Lugar, Petersen, & Schlaggar, 2003), all brains were spatially normalized to the same standardized space (SPM99 EPI template) (Woods, Cherry, & Mazziotta, 1992). Spatial normalization warps brains into Talairach space so that all brains are the same size and shape for comparison.

Group Face Localizer Analysis

Group analyses of the face localizer tasks were conducted for data in each experimental chapter. For group analyses, individual brains were warped into a standardized space for the detection of common activity within groups and global differences between groups. Four condition mean images for the four experimental conditions (F, M, N, fix) were computed for each subject and then spatially normalized using warp algorithms of AIR, yielding images with 2 mm^3 resolution. For each age group (5-8 years, 9-11 years, and adults), paired t-tests with subjects as a random effect yielded twelve group statistical maps which were converted into z maps: F>M, F>N, F>fix, fix>M, fix>N, fix>F, N>M, N>F, N>fix, M>N, N>F, and N>fix. To test for specific brain activation patterns using logical combination (Joseph et al., 2002) the z maps were combined using logical operators (AND = &, OR = |, NOT = ~) in the image calculator of Medx. Refer to Appendix A for details.

Individual Face Localizer Analysis

Individual analyses of the face localizer data were performed in Chapters Five and Six. Because normal developing children may use different cognitive strategies or neural networks to perform a task, we conducted individual subject analyses to identify variability that might be lost in a group analysis (Gaillard, Grandin, & Xu, 2001a). For individual analyses, unpaired t-tests of stimuli conditions (F, M, N, fix) produced the 12 unique contrasts of interest (z maps). As in the group analysis, we conducted further analyses using the logical combination approach (Joseph et al., 2002).

Pediatric Shape-Matching Task Design and Stimuli

For the shape-matching task (Figure 3.1), 12 three-dimensional line drawings known as geons (Biederman, 1987) were used as stimuli. Non-matching stimulus pairs or "different" trials were created by determining the number of shared non-accidental properties between two shapes. See Figure 2.2b. Shared non-accidental properties were classified along four dimensions: 1.) edge of the cross section (straight or curved); 2.) symmetry of the cross-section (rotational, reflectional, or both); 3.) size of the cross section along the longitudinal axis (expanded or constant); and 4.) edge of the longitudinal axis (straight or curved) (Biederman, 1987). Ten stimulus pairs were created for each of three structural similarity (SS) levels, with SS1 indicating one shared non-accidental property and SS3 indicating three shared properties. Within each 9- minute functional run, 9 pseudorandomly ordered task epochs (3 of each SS level), were interleaved with 8 fixation blocks. Each epoch consisted of 30 pseudorandomly ordered stimuli presented for 2500 ms each followed by a fixation crosshair presented for 500 ms. Each epoch contained "different" pairs representing only one SS level while "same" pairs were randomly assigned to each block. Fixation blocks consisted of a stationary black cross-hair centered on a white background. Participants were instructed to view the pictures and push a button beneath their index finger each time they saw a "same" pair and to push a button beneath their middle finger each time they saw a "different" pair. Before entering the scanner, participants viewed "same" shape pairs for as long as they needed to learn correct matches and then had 24 practice trials. Training reduced ambiguity about what constituted a stimulus match and provided assurance that the pediatric subject could perform the task.

Adult Shape-Matching Task Design and Stimuli

The adult and child face localizer task were identical. However, for shape-matching, adults completed only one twelve-minute functional run with 12 task blocks and a stimulus presentation time of 400ms/pair followed 1600ms of fixation. Fixation and shape stimuli were identical to those in the pediatric design. As with child participants, training preceded scanning to ensure that adults understood the task.

FMRI Shape-Matching Analysis

For the shape-matching task, 10 condition mean images (three repetitions of three experimental conditions -- SS1, SS2, SS3 – plus a fixation mean) were computed for each run for each subject and then spatially normalized yielding images with 2 x 2 x 2 mm resolution. These images were averaged across runs for a subject and submitted to subsequent analyses. To test for activation patterns driven by the parametric manipulation of SS, two cross-correlation analyses were performed. As with face localizer data, shape-matching data was assessed at the group and individual levels.

Group Shape Analysis

The group-level time series was cross-correlated with two distinct reference waveforms: 1.) one waveform to determine areas showing fMRI-signal increases with high SS levels, and 2.) one waveform to determine areas showing a greater fMRI signal with low SS levels. From the cross-correlation analyses, clusters of activation modulated by SS levels served as regions of interest (ROIs). Within each ROI, percent signal change for each SS level (SS level – fixation) for each subject was submitted to a repeated measured ANOVA to assess the effect of SS on fMRI signal within each cluster. Finally to compare child and adult activation, ROI clusters were overlaid onto the SPM T1-weighted anatomic brain template. ROI**'s** reported were significant for the group-level cross-correlation ($z > 2.33$, $p < .01$) and showed consistent effects across subjects in the repeated measures ANOVA ($p < .05$).

Individual Shape Analysis

Using the same reference waveforms as in the group analyses, individual subject cross-correlations were performed to determine what brain regions were modulated by SS. Like the group analysis, resulting clusters were thresholded at a z score of 2.33 (some at 1.64 in cases where few clusters were detected at $z > 2.33$) and served as ROIs. As in the face localizer task, individual analyses provided information on inter-subject variability.

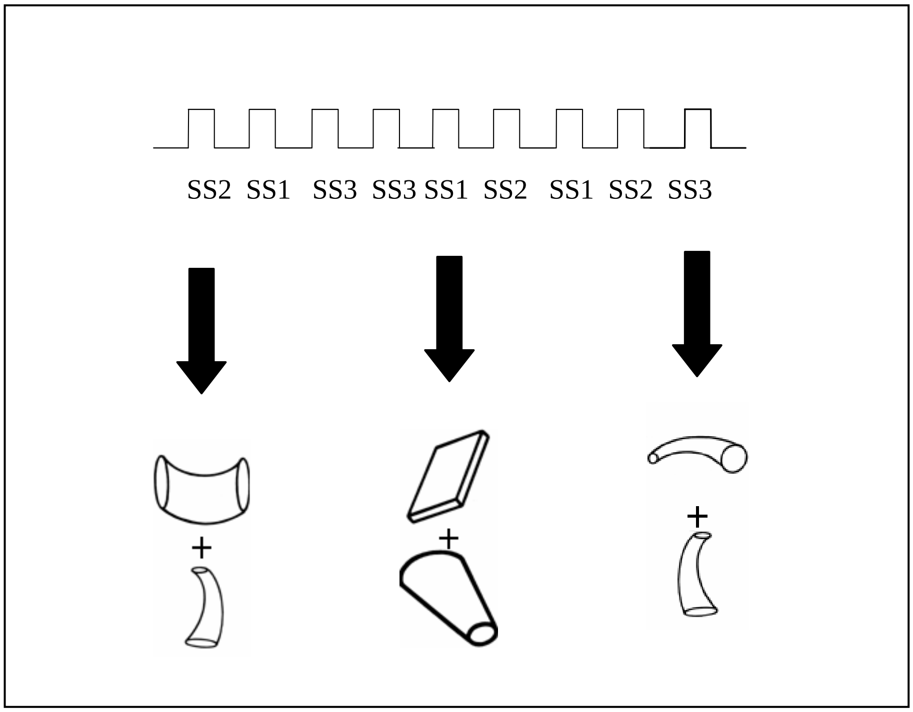


Figure 3.1. Shape-matching task design & example stimuli for "different" trials. "Different" pairs within a block are dedicated to one level of structural similarity (SS). SS1 = least similarity. SS3 = greatest similarity.

Chapter Four: Developmental shifts in cortical loci for face and object recognition

Summary

Information on normal functional organization and development of the ventral processing stream in 5-11 year old children is minimal. The present fMRI study identified neural correlates for face and object processing in children 5-8 and 9-11 years, with data from a similar adult study (Joseph & Gathers, 2003) used for comparison. All age groups showed face-preferential activation in the ventral processing stream, but adults and children 9-11 years showed face-preferential loci near the classically defined fusiform face area, whereas children 5-8 years showed this activation in the posterior ventral processing stream. In addition, the degree of category-selectivity in other brain regions increased with age. Collectively, these developmental changes may reflect fine-tuning in visual recognition processes based on learning and experience.

Introduction

As discussed in Chapter 1, the ventral processing stream is a functional pathway in the primate brain that supports visual recognition. The functional organization of this pathway remains a controversial topic. Studies of damaged and healthy adult brains (Damasio, 1990; Haxby et al., 2001; Joseph & Gathers, 2002; Kanwisher et al., 1997) yield two divergent hypotheses concerning the functional architecture of the ventral processing stream. One view posits that ventral processing stream organization is based on neural specializations, or modules, dedicated to the processing of particular categories (Kanwisher et al., 1997). An opposing view is that the ventral processing stream is characterized by overlapping regions sensitive to the recognition of multiple categories (Haxby et al., 2001; Joseph & Gathers, 2002). In support of the modular view, the fusiform face area, an anterior region of this pathway, appears to be specialized for face recognition (Kanwisher et al., 1997). However, in support of neural generalization, our previous adult study demonstrated that the fusiform face area was not selective for faces but exhibited a graded response in which faces produced a greater response than did objects, but objects produced a statistically greater response than baseline (Joseph & Gathers, 2002). In fact, face-selective responses, those in which categories other than faces did not activate the region significantly more than baseline, were absent within this processing stream.

Further controversy focuses on whether the functional organization of the ventral processing stream is predetermined and early-established (Farah et al., 2000; Gilchrist & Mckone, 2003; Morton & Johnson, 1991) or sculpted by experience and learning over time (Gauthier & Nelson, 2001; Pascalis & Slater, 2003). Farah (2000) and Gilchist and McKone (2003) propose early-established (prior to age 3) face and object recognition systems whereas both Carver et al. (2003) and Passarrotti et al. (2003) suggest changing neural architecture from childhood to adulthood. To delineate the neural correlates of face and object recognition at different developmental stages, we compared brain activation patterns of children 5-8 years, 9-11 years, and adults who passively viewed blocks of faces, natural objects, and manufactured objects, similar to tasks implemented in previous studies (Joseph & Gathers, 2002; Kanwisher et al., 1997). One goal of the present study was to examine the cortical locus of face responsive regions throughout development. The classically defined fusiform face area falls in the anterior fusiform gyrus but a posterior locus is also often reported (Joseph & Gathers, 2002; Kanwisher et al., 1997). To isolate the fusiform face area, we defined face-preferential activation as a statistically stronger response to faces than to both object categories and to baseline but object responses were not statistically constrained relative to baseline. Our question was whether the classically defined fusiform face area (i.e. a face-preferential response in the anterior fusiform gyrus) emerges in all age groups. Based on other developmental fMRI studies of face processing (Gilchrist & Mckone, 2003), language (Holland & al., 2001; Schlaggar & al., 2002), and working memory (Thomas et al., 1999) that confirm similar cortical regions of activation in school-aged children and adults, it is likely that the functional organization of the ventral processing stream is stable across the ages we are studying.

Another goal was to determine whether face-preferential activation is exclusive for faces (face-selective) or whether other object categories (i.e. manufactured and natural objects) also activate face-preferential regions to a statistically significant degree relative to baseline (graded-activation). If face-preferential activation is not exclusive for faces, then it should spatially overlap more with face-graded activation than with face-selective activation, as previously reported in adults (Joseph & Gathers, 2002). We tested the developmental stability of these functional activation profiles from 5-11 years of age.

A final goal was to determine whether developmental changes are unique to a particular object category (i.e. faces, natural objects, and manufactured objects). To that end, we also isolated brain regions that were selective for natural or manufactured objects and compared the degree of category-selectivity across age groups.

Participants

Child Subjects

Twenty-nine 5-11 year old healthy children (18 males, 11 females, mean age 8.3 years) with no significant medical histories were compensated for participation. All volunteers had normal visual acuity, were fluent in English, and showed a right-hand preference based on the Edinburgh Handedness Survey. Receptive and expressive language skills were within normal age limits as determined by the Peabody Picture Vocabulary Test (Dunn & Dunn, 1997) and the Expressive Vocabulary Test (Williams, 1997). Three children did not complete the study. Data from six other participants were omitted due to excessive head motion. Thus, data from 20 subjects (12 males, 8 females, mean age 8.8) were submitted to further analyses.

Adult Subjects

Nine adults (five males, mean age 20.8 years, one left-handed) with normal or corrected-to-normal vision and no significant medical or psychological conditions participated in a previously published study (Joseph & Gathers, 2002). The adult data were submitted to additional analyses and used to compare with the pediatric data in this study.

Results

To localize the fusiform face area, we isolated face-preferential activation in all three age groups. Adults showed two bilateral foci of face-preferential activation in the ventral processing stream; one focus in the classically defined fusiform face area [anterior aspects of the fusiform gyrus in Brodmann's Area (BA) 37 and a more posterior fusiform locus in BA 18, as we previously reported (Joseph & Gathers, 2002) (Figure 4.1a). Children nine to eleven years showed face-preferential activation in the right anterior fusiform gyrus (BA 37; x = +42, y = -56, z = -22), close to the classically defined fusiform face area (Figure 4.1b). Face-preferential activity in children 5-8 years emerged in the right (BA 17; x = +28, y = -96, z = -14) and left occipital gyri (BA 18; x = -32, y = -85, z = -19) as shown in Figure 4.1c.

As in our previous study (Joseph & Gathers, 2002), we were interested in whether face-preferential regions are better characterized by graded or selective responses to faces to assess the degree of specialization in the fusiform face area. In all three age groups, face-preferential activation (blue voxels in Figure 4.1) overlapped primarily with face-graded responses (yellow voxels) and minimally with face-selective activation (red voxels). A repeated-measures ANOVA examined the effect of overlap (preferential-graded v. preferential-selective) and age on the number of voxels that overlapped throughout the brain. Extent of face-preferential and face-graded overlap (19.5% of preferential voxels were also graded voxels) was greater than extent of face-preferential and face-selective overlap [2.3%; $\underline{F}(1,26) = 14.6$, $\underline{p} < .001$]. Neither the age effect nor the Age x Overlap interaction was significant. Hence, the functional characteristics of face-preferential regions do not change after age five. Moreover, face-preferential activation, including the classically defined fusiform face area, does not reflect specialized activation for faces.

Although the ventral processing stream did not show category-selective activation, the degree of category-selectivity increased with age in other regions of the brain. Five to eight year old children had no selective activation for any object category whereas children 9-11 years had selective activation for each category: natural objects (right inferior parietal lobe, bilateral middle frontal gyri), manufactured objects (left temporal pole, right inferior frontal gyrus), faces (left inferior frontal gyrus). Adults also showed distinct regions of category selectivity: natural objects (left superior parietal lobule, left temporal pole), manufactured objects (right calcarine sulcus, right middle occipital gyrus), and faces (left hippocampus). Although these selective brain regions were small and few, percent of face-selective voxels throughout the brain relative to the total number of voxels for face-graded, conjoined, and object-selective activation increased from 0% in children 5-8 years to .14% in children 9-11 years to .41% in adults.

Finally, we defined conjoined activation as statistically equivalent responses to all stimulus categories in our study relative to each other, and significantly different responses for each category relative to baseline. This non-category specific activation dominated other task-relevant forms of activation for all three age groups. For adults, 84% of total activated voxels were conjoined (i.e. relative to all six profile types combined), 89% for children 9-11 years, and 74% for 5-8 year old children. The bulk of conjoined activation fell within the ventral processing stream.

Discussion

The present study contributes several new findings to our understanding of ventral processing stream development. First, only adults and children ages 9-11 years showed face-preferential responses near the classically defined fusiform face area, whereas 5-8 year old children only showed face-preferential responses in the posterior ventral processing stream. These differences in cortical locus for face processing are not due to greater head motion in children because corrected head motion was equivalent for all age groups. Instead, changes in ventral processing stream locus for face processing may be due to a variety of developmental factors. Shifts in face-preferential loci may result from maturation of neural pathways and connections. For example, visual recognition may be facilitated by connections to the frontal lobe (Bar, 2003; Vogels, Sary, Dupont, & Orban, 2002), a later developing region of cortex (Luna et al., 2001). Hence, shifts may occur in the neural architecture of the ventral processing stream to accommodate maturation of frontal lobe connections. In addition, behavioral studies (Carey & Diamond, 1994; Schwarzer, 2000) have suggested developmental changes in cognitive mechanisms for face recognition. Interestingly, around 10 years of age, children display more adult-like strategies for face recognition (Carey & Diamond, 1994). Our data suggest that this change in cognitive processing may be accompanied by an anterior shift in the ventral processing stream locus for face recognition because only adults and 9-11 year old children activated the anterior fusiform gyrus during face recognition, whereas younger children did not.

Second, the functional activation profiles of face responsive brain regions did not change with age. Specifically, for all age groups face-preferential activation in the ventral processing stream significantly overlapped with face-graded activation but never with face-selective activation. Although the cortical locus of face-preferential activation changed with age, regions showing face-preferential responses did not show exclusive responses for faces. Rather, other object categories also activated these regions to a significant degree. In addition, neither fMRI signal strength nor variability changed systematically across development. Five to 8 year old children produced stronger fMRI signals in some regions than adults, and between-subject variability in signal strength (reflected by standard error bars in Figure 4.1d-f) was not markedly different across age.

Third, no category selective regions emerged within the ventral processing stream but they emerged in other brain regions for children 9-11 years and for adults. The emergence of category-selective clusters with age may be due to plasticity driven by learning and experience (Gauthier & Nelson, 2001). Moreover, other studies suggest that “category-selective” processing may require recruitment of cortical regions other than the ventral processing stream (Vogels et al., 2002). The present data support this by showing that much of the ventral processing stream in childhood as well as in adults was explained by conjoined and graded activity, both of which reflect non-category specific responses. An alternative explanation for the failure to find selective activation in the 5-8 year old children is that the cortical locus for category-selective activation is more variable at this age and is, thus, more difficult to detect in group-averaged maps. In fact, another developmental fMRI study reports more distributed VPS processing in children than in adults (Passarotti et al., 2003). However, this variability in and of itself may reflect fine-tuning of neural circuitry with development of expertise.

We (Joseph & Gathers, 2003) and others (Gauthier, Tarr et al., 1999) have suggested that face-preferential responses in the ventral processing stream may not reflect taxonomic category distinctions per se, but instead reflect a process of differentiating members of object categories that are highly perceptually similar or similar in shape. We have further suggested that if more perceptual differentiation is required (as in face recognition), then a relatively more anterior ventral processing stream locus of activation will emerge. Hence, an anterior shift in the ventral processing stream locus for face processing with age may support more skilled perceptual differentiation of objects that are highly similar (Carey & Diamond, 1994) in shape, such as faces. This anterior shift may emerge around the time that face processing skills become more adult-like (around 10 years of age).

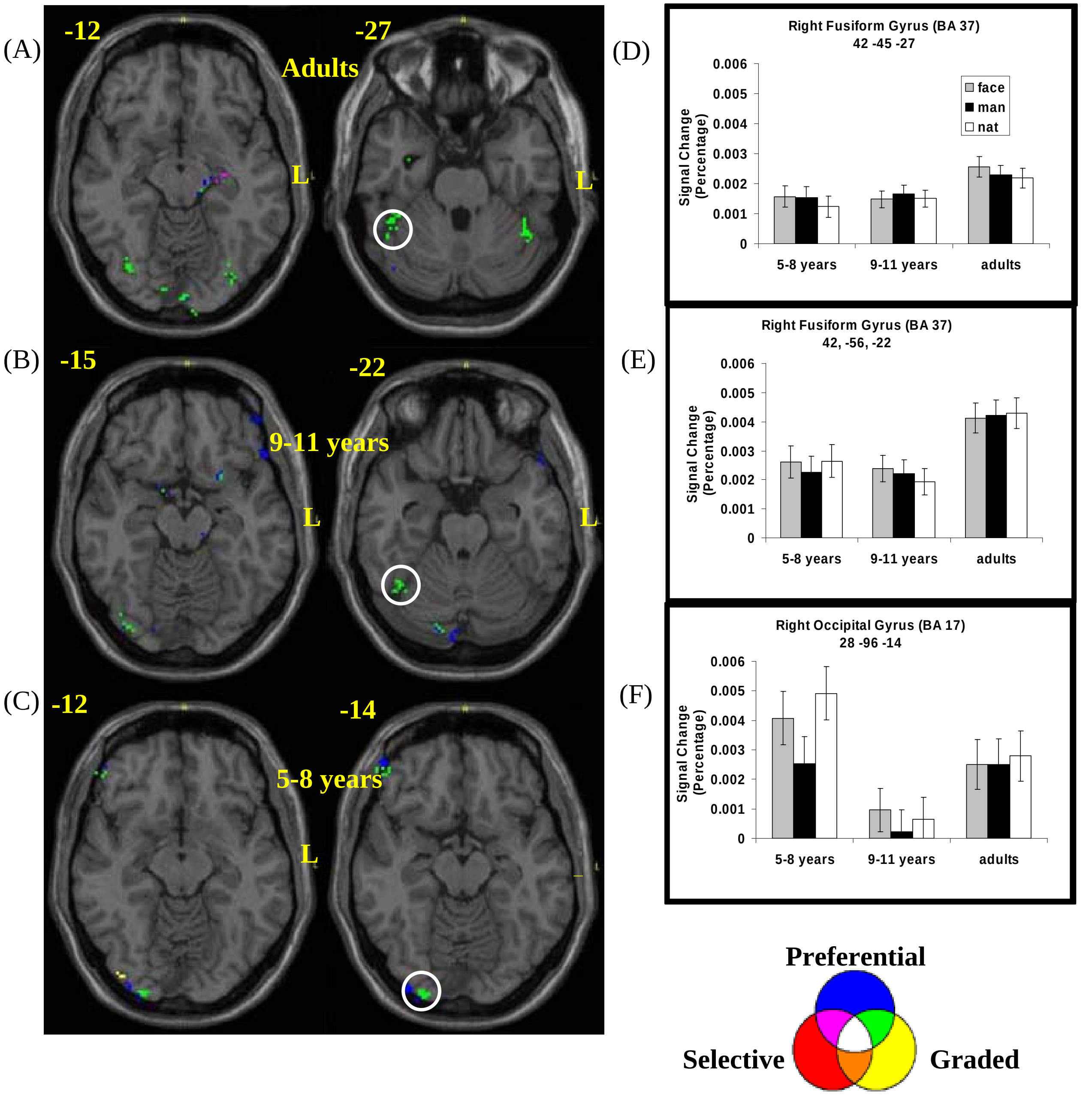


Figure 4.1. Two axial slices of ventral brain regions in (A) adults, (B) 9-11 years and (C) 5-8 years. MNI space z-coordinate in the upper right corner. Face-preferential activation (blue); face-graded activation (yellow); face-selective activation (red). Percentage fMRI signal change as a function of age and condition (F, M, N) is shown for one region (white circle) in each age group: (D) right fusiform gyrus BA (37) region in adults; (E) right fusiform gyrus BA (37) region in 9-11 years; (F) right occipital gyrus BA (17) region in 5-8 years. Error bars reflect standard error of the mean. Copyright 2004 Lippincott Williams & Wilkins.

Chapter Five: Neural Correlates of Structural Similarity Processing Emerge in the Human Ventral Processing Stream After Eight Years of Age

Summary

The current set of experiments used fMRI to investigate maturational changes in the functional organization of the VPS responsive to a structural similarity (SS) mechanism of object recognition. Imaging and behavioral data were collected during a visual recognition task in which 5-8 year olds, 9-11 year olds, and adults made same/different judgments for shape pairs with parametrically varied levels of SS. Error rates from combined same/different trials indicated sensitivity to SS modulation across all age groups. Performance was worse for children and adults on the highest SS pairings (SS3) compared to lower SS pairs. Developmental differences existed in bias measures. Criterion settings for high SS pairs grew increasingly liberal with age, reflecting maturational changes in processing strategies. Imaging data revealed that bilateral VPS regions sensitivity to high SS emerged after eight years of age whereas no VPS regions showed sensitivity to low SS at any age. Bias and functional results together indicate the changes in SS processing strategies and corresponding neural substrates after age eight. In a second set of experiments, SS brain images were compared with data from the passive face and object viewing experiment in Chapter Four. Based on the high structural resemblance among human faces, we hypothesized that SS played a role in the development of face recognition. The results did not support our hypothesis.

Introduction

As discussed in the preceding chapters, the functional organization of the ventral processing stream (VPS) is controversial and has been attributed to multiple factors including: taxonomic category (Kanwisher et al., 1997), level of categorization (superordinate, basic, and subordinate) (Gauthier et al., 1997), expertise (Gauthier, Skudlarski et al., 2000), and relational (holistic, configural, global) versus featural (piece-meal, analytical, local) processing (Lerner, Hendler, Ben-Bashat, Harel, & Malach, 2001; Moses et al., 2002). Structural processing offers another possible mechanistic explanation for VPS functional organization (Gerlach, Aaside et al., 2002; Gerlach, Law, & Paulson, 2004; Joseph & Gathers, 2003; Price, Noppeney, Phillips, & Devlin, 2003). In the current chapter, we investigate the development of the VPS from a structural processing standpoint and pose two experimental questions: 1.) Do age-related changes occur in the VPS neural substrates of structural processing? 2.) Do functional changes in structural processing explain developmental shifts in the VPS neural correlates for face processing?

Object Recognition – Structural Processing Theories

In most theories of object recognition (Biederman, 1987; Humphreys, Riddoch, & Quinlan, 1988; Marr & Nishihara, 1978), structural processing refers to the existence of an intermediate, pre-semantic stage of object processing involving visual shape representations. According to Biederman's Recognition-By-Components Theory (RBC) (Biederman, 1987), shape representations are three dimensional abstract object forms called structural descriptions. Each structural description can be dissected into primitive volumetric components called geons. It is the unique combination of type, size, and spatial arrangement of geons that characterize an object's identity (Biederman, 1987). In another account of object recognition, Edelman and colleagues propose that the relative shape similarity between objects rather than an object's own unique shape representation determines identity (Edelman, 1995; Edelman, Bulthoff, & Bulthoff, 1999; Edelman & Duvdevani, 1997). In other words, new external objects are compared to a small, diverse set of learned prototypes (i.e. active landmarks) and "recognized" based on the amount of resemblance between the objects and the prototypes. Though these theories differ in many ways, both theories pose abstract shape representations as the basis of object recognition.

A Structural Explanation for Category-Specific Deficits

Across studies, researchers have emphasized the role that structural characteristics of stimuli play in the organization of the cortex for visual processing (Arguin, Bub, & Dudek, 1996; Damasio et al., 1982; Humphreys & Riddoch, 2003; Joseph & Gathers, 2003; Price, Noppeney et al., 2003; Price, Winterburn, Giraud, Moore, & Noppeney, 2003; Tranel, Damasio, & Damasio, 1988; Tranel, Damasio, & Damasio, 1997). As noted in Chapter 1, category-specific recognition deficits corresponding to lesions in specific cortical regions serve as evidence for taxonomic organization of the VPS. However, Damasio suggested that, though deficits and corresponding lesions support differentially dedicated neural processing, neural systems are not dedicated to processing conceptual categories but rather to processing perceptual properties of stimuli (Damasio, 1990). In their analysis of lesion data, Damasio and colleagues concluded that the face recognition impairment, prosopagnosia, was not limited to faces but extended to any visually ambiguous stimuli where visual ambiguity was defined by members of a group of stimuli sharing similar forms (Arguin et al., 1996; Dale & Buckner, 1997; Damasio et al., 1982; Gaffan & Heywood, 1993; Humphreys & Riddoch, 2003; Price, Noppeney et al., 2003; Price, Winterburn et al., 2003; Tranel et al., 1988; Tranel, Damasio et al., 1997). Other studies of face and non-face agnosia support Damasio's suggestion of a structural similarity (SS) basis for visual processing (Arguin et al., 1996; Gaffan & Heywood, 1993; Humphreys & Riddoch, 2003; Tranel et al., 1988). An investigation of visual processing revealed faulty processing of structural knowledge in a man with a "living-things" agnosia and bilateral inferior temporal damage (Arguin et al., 1996). Using line drawings of fruits and vegetables in a picture/word matching task, the authors found that the gentleman failed to process shape features necessary to identify the target among structurally related stimuli. This finding was verified by similar performance on a visual recognition task involving controlled manipulations of shape stimuli dimensions (i.e. curvature and linearity). Taken together, these studies imply a structural similarity (SS) basis for object recognition where structural similarity refers to the degree of differentiation between two structural descriptions.

Studies of Structural Processing in Healthy Adults

Behavioral (Tranel, Logan, Frank, & Damasio, 1997) and imaging studies (Gerlach, Law, Gade, & Paulson, 2002; Gerlach et al., 2004; Joseph & Gathers, 2003; Price, Noppeney et al., 2003; Tranel et al., 2003) of unimpaired subjects provide further support for a structurally-driven visual recognition system. Others also investigated the impact of structural similarity (visual ambiguity or homomorphy) on visual recognition in normally functioning adults (Tranel, Damasio et al., 1997; Tranel, Logan et al., 1997). The authors proposed seven possible factors, including familiarity and SS, which may determine visual processing dissociations. Normal subjects rated stimuli from multiple categories (i.e. animals, fruits/vegetables, tools, vehicles, and musical instruments) on each of the seven factors. Analysis of the ratings indicated that high SS accounted for a large extent of visual recognition distinctions. Thus, behavioral data of normal subjects support an SS basis for apparent category-related dissociations in visual recognition.

In a PET study, Tranel et al. identified occipito-temporal correlates of animal naming from the auditory presentation of the animals' sounds (2003). Based on their previous findings, they reasoned that recruitment of the visual association cortex by the task reflected top-down retrieval of physical structure knowledge about the animal being named. Similarly, using PET, Price and colleagues found that the lateral occipital complex, a structurally sensitive object processing region in the VPS, was differentially activated by varying degrees of structural similarity inherent to living versus non-living object categories (2003). Therefore, PET studies have produced evidence for a structurally-based organization within the VPS.

Using fMRI with adult participants, we investigated the effect of structural similarity (SS) on VPS neural activity by parametrically varying the amount of structural overlap (low to high similarity) between two object stimuli (pairs of animals or pairs of three dimensional shapes). As subjects performed a same/different matching task on these SS pairs, we measured fMRI signal changes, reaction times, and error rates. Reaction times and error rates increased as a function of SS indicating structural demands on object processing. Corresponding imaging data revealed neural correlates of structural processing with activation by low SS in posterior ventral processing stream (VPS) regions and sensitivity to high SS in mid-anterior VPS regions (Joseph & Gathers, 2003). In addition, mid-anterior fusiform regions, in close proximity to regions previously identified as specialized for face recognition (i.e. the fusiform face area, Kanwisher et al., 1997), were sensitive to high structural similarity. Thus, a structurally-driven recognition system is a reasonable alternative to categorically-driven functional organization of the VPS in adults.

The Importance of Structure in Object Processing

Behavioral and imaging literature in normal and disordered adults emphasizes the importance of structure in object processing. As mentioned at the beginning of this chapter, the idea of structural representations is central to most object recognition theories. Shape is an important aspect of perception. Even newborns show evidence of simple form perception. For example, using a novelty preference task, Turati et al. found that newborns rely on shape similarity to form broad categories of geometric shapes (2004) and, in a similar task, Slater et al. discovered infants were sensitive to changes in angle (i.e. obtuse or acute) (1991). Similarly, infants are sensitive to the same cues that adults use to derive three-dimensional images. Three month old children detect differences in shading (Bhatt & Waters, 1998) and selectively attend to holistic combinations of line intersections in 3-D static images (Bhatt & Bertin, 2001). At 4.5 months infants use shape similarities and differences to individuate objects in occlusion events (Wilcox, 1999) and, beginning as early as 18 months, a shape bias is linked to object naming (Landau, Smith, & Jones, 1998; Samuelson & Smith, 1999). Though these findings indicate that structure is important in human object perception, these data do not predict whether infants and young children use shape information to the same degree as adults.

Evidence that Development "Shapes" Object Recognition

To ascertain the function of an early-established shape-sensitive object recognition system, many behavioral studies have investigated the development of structural processing. Early cognitive studies indicate that children and adults differ in their perception of shape. Piaget and Inhelder found that three and four year olds failed to perceive Euclidean relations when asked to draw simple shapes (1948). Not until nine or ten years of age did children code metric distances to produce accurate representations of geometric forms. These developmental changes in geometric concepts indicated that young children use spatial relations in a fundamentally different way than adults. Another marked difference in shape perception between children and adults was reported by Gibson et al. (1962). The authors found that four year olds, unlike 8 year olds, did not discriminate between curved and straight lines to distinguish among variations in letter-like forms.

More recent studies also support maturational changes in structural processing. In a series of object recognition experiments, Abecassis and colleagues used perceptual rating, memory and matching tasks to investigate what dimensional strategies children and adults use for object discrimination and identification (2001). Similar to the Gibson et al. finding in 8 year olds (1962), the authors found that adults extract dimensional information such as curvature and parallelism for perceptual similarity judgments. Furthermore, in line with Piaget and Inhelder's (1948) account of spatial relationship development, results indicated that adults used metric relationships to perform similarity ratings. Using memory and matching tasks, the authors found that when identifying objects, children and adults do not represent shape dimensions in the same manner. There is a developmental transition from a perceptual similarity continuum to categorical representations of dimensions. These developmental changes may be due to increased selective attention to stimulus differences (Gibson, 1969) or a learned dimensional value weighting strategy (i.e. classifying stimuli according to a particular dimension such as curvature to facilitate identity judgments) (Smith & Evans, 1989).

Developmental changes in selective attention to shape are noted in other object recognition studies. In general, a maturational shift in attention to shape has been noted in various naming tasks (Gershkoff-Stowe & Smith, 2004; Landau, Smith, & Jones, 1988). Overall, these studies reported the existence of a shape bias that increases with age. In another object naming task, Smith found qualitative changes in object recognition from 17 months to 25 months of linked to category learning. When tested with real objects and caricature shapes of the same objects (composed of geon-like parts), young children with limited vocabulary did not recognize the caricatures. Smith attributed this inability to recognize caricatures to the lack of an abstract structural representation. In contrast, children with slightly more advanced vocabulary performed well on caricature shape recognition. Hence, she inferred that shape representations are developmental products of category learning (Smith, 2003). Whether attention or learning is involved in the shaping of structural representations from childhood to adulthood, from these and other studies, there are reasons to believe that children and adults process structure differently.

Current Investigations

Based on this supposition, we ask two questions in the current investigation: 1.) Do changes in the neural substrates of structural similarity processing occur with age? 2.) Can developmental changes in face processing be explained by structural processing? Though the development of structural processing has been investigated from a behavioral standpoint, to our knowledge, no previous functional imaging studies have focused on developmental changes in the neural correlates of structural object processing. In the current study, we sought to determine if changes in a structural-based mechanism could account for the development of VPS organization. Children 5-8 years and 9-11 years of age participated in a shape-matching fMRI experiment similar to our previous adult study (Joseph & Gathers, 2003). Again, we parametrically varied the degree of structural similarity (low SS to high SS) within 3-D shape pairs. Children decided if two simultaneously presented shapes were the same. In the present analyses, we evaluated and compared pediatric data to adult findings to determine if the functional activation in the VPS of children during visual object processing, as in adults (Joseph & Gathers, 2003), is modulated by structural similarity.

In addition to examining maturational changes in shape processing, we evaluated the face-sensitive VPS regions of children and adults for indications of SS processing. Based on data supporting structurally driven functional organization of the VPS for visual recognition, we proposed a structural similarity mechanism for face processing. To test our proposal, we overlaid our shape-matching results with results from a passive face and object-viewing task. Applying the logical combination analysis to the passive viewing task (Joseph et al., 2002), we isolated face-preferential regions characterized by statistically greater fMRI signal to face stimuli than non-face object stimuli and baseline. Considering that faces are highly similar in their overall structure, we reasoned that an overlap of face-preferential regions with neural correlates sensitive to structural similarity, in particular high SS, would confirm a structural rather than a categorical basis for face processing.

We expected developmental differences in structural similarity processing to explain developmental shifts in face processing loci. Behavioral and physiological measures have shown that face processing undergoes developmental changes (Carey & Diamond, 1977; Carey & Diamond, 1994; R.J. Itier & M.J. Taylor, 2004; Maurer et al., 2002; Mondloch et al., 2002; Mondloch et al., 2003; Pellicano & Rhodes, 2003; Schwarzer, 2000; Want et al., 2003). To date, neuroimaging data provide further support for age-related changes in face processing (Aylward et al., 2005; Gathers, Bhatt, Corbly, Farley, & Joseph, 2004; Joseph, Gathers, Liu, Corbly, & Whitaker, submitted; Passarotti et al., 2003). Previously, we identified developmental shifts in face-preferential (face-sensitive) regions in children ages 5-8 years, 9-11 years, and adults participating in a passive face and object viewing task. Face-preferential activation occurred in bilateral posterior VPS regions of 5-8 year olds, while 9-11 year old children recruited more anterior right fusiform regions, and adults activated bilateral posterior and anterior regions of the VPS. The face preferential regions identified in the right anterior fusiform of adults and 9-11 year olds corresponded with a high SS processing region identified in a previous adult study (Joseph & Gathers, 2003). No such regions were identified in 5-8 year olds. Thus, we hypothesized that as children mature they increasingly rely on structural differentiation for face processing. Here we discuss our findings regarding SS development in the VPS and their relevance to face processing development.

Participants

Child Subjects

Twenty-nine 5-11 year old healthy children (18 males, 11 females, mean age 8.3 years) with no significant medical histories were compensated for participation. All volunteers had normal visual acuity, were fluent in English, and showed a right-hand preference based on the Edinburgh Handedness Survey. Receptive and expressive language skills were within normal age limits as determined by the Peabody Picture Vocabulary Test (PPVT) (Dunn & Dunn, 1997) and the Expressive Vocabulary Test (EVT) (Williams, 1997). Three children did not complete the study. Data from three other participants were omitted due to excessive head motion. Thus, data from 23 subjects, subdivided into ten 5-8 year olds (8 males, mean age 7.4 years) and thirteen 9-11 year olds (6 males, mean age 10.7), were submitted to further analyses.

Adult Subjects

Sixteen adults with normal or corrected-to-normal vision and no significant medical or psychological conditions participated in a previously published study (Joseph & Gathers, 2003). Data from 6 participants were omitted due to excessive head motion or image artifacts. The remaining data from 10 adults (5 males, mean age 24.5 years, 9 right-handed) were submitted to additional analyses and compared with the pediatric data in this study.

Results

Behavioral Results

For the shape-matching task, we assessed error rates (Figure 5.1), reaction times (Figure 5.2), sensitivity and bias (Figure 5.3a & b). Only correct log reaction times (RT) within three standard deviations of the group mean were submitted to further analyses. We evaluated the effect of same/different trials on error rates and reaction times. Considering that no parametric manipulation of SS occurs on "same" trials ("yes" responses), assessment of same/different functions verifies affects of experimental manipulations. In addition, same/different response functions may provide information regarding potential maturational differences in processing strategies (Gathers, Bhatt, & Joseph, 2004). We submitted our data to a mixed, two-way, repeated-measures ANOVA in which SS level (SS1-SS3) and Same/Different responses (yes and no) served as within-subject factors and Age (5-8 years, 9-11 years, and adults) served as the between-subjects factor. Overall, error rates [$F(2,56) = 25.8$, $p < .000$] and reaction times [$F(2,54) = 37.2$, $p < .000$] increased with increasing SS levels. In addition, the main effect of same/different responses was significant for error rates [$F(1,28) = 36$, $p < .000$] and reaction times [$F(1,27) = 45.5$, $p < .000$] as was the interaction of Same/Different x SS level for both measures ([$F(2,56) = 34.9$, $p < .000$] and [$F(2,54) = 13.4$, $p < .000$] respectively). As expected, error rates and reaction times increase as a function of SS level for "different" responses but not for "same" responses verifying our manipulation of SS. This is consistent with other studies that manipulated SS (Humphreys et al., 1988; Joseph & Farley, 2004; Joseph & Gathers, 2003; Joseph & Proffitt, 1996).

For the main effect of age, reaction times [F(2,27) =37.6, p < .000], but not error rates [F(2,28) = .89, p < .422], decreased as a function of age with adults taking less time to respond than both child groups. Thus, children were slower to respond than adults but their overall error rates were not significantly different than adults. Hence, the absence of a main effect of age for errors revealed that our shape-matching experiment was equated for performance, in regards to accuracy, across age groups. Overall, reaction time and error rate results indicated that adults respond faster than children at the expense of more errors.

The three-way interaction of SS level x Same/Different x Age was significant for error rates [F(4,56) = 4.5, p < .003]. For “different” pairs, all ages show an effect of SS in error rate (see Figures 5.1 and 5.2). In children and adults, similarity judgments were more difficult for the most structurally similar pairs. All ages produced more errors at SS3 than other SS levels with adults demonstrating the greatest increase in errors from SS2-SS3. Thus, error data indicated 5-8 year olds, 9-11 year olds, and adults used a structural similarity mechanism for the current shape-matching task. The same three-way interaction was not significant for reaction time [F(4,54) = 1.7, p < .168]. Figures 5.3 and 5.4 depict two-way ANOVA results for reaction times.

Higher sensitivity measures indicate greater discrimination between “same” and “different” stimuli. A sensitivity measure of .5 indicates chance performance – no discrimination between “same” and “different” stimuli. Bias measures, ranging from -1 to 1, reflect criterion settings. Negative bias values indicate a liberal criterion to respond “same” and positive values indicate a conservative criterion to respond “different”. Overall, highly similar pairs (SS3) were associated with poor discrimination between “same” and “different” pairs [F(2,27) = 55.1, p < .000] and a tendency to respond “same” [F(2,27) = 71.9, p < .000]. Poorer discrimination at SS3 than SS1 is consistent with the main effects of level in error rates. The main effect of age was not significant for sensitivity [F(2,28) = .727, p < .603]. Thus, overall, adults and children discriminate equally well. For all ages, the most structurally similar pairs were the most difficult to discriminate. However, the analysis of bias indicated significant changes in criterion settings with age [F(2,28) = 5.5, p < .010]. The interaction of SS level x Age was also significant for both sensitivity [F(4,54) = 6.9, p < .000] and bias [F(4,54) = 6.7, p <

.000]. For adults, simple main effects indicated an increasingly liberal bias for SS3 trials compared to SS1 and SS2. Overall, adults were less sensitive and more liberal in their high SS responses than both child groups (see Figure 5.5). Bias and sensitivity were not correlated (r = -.042).

Imaging Results

VPS Regions Modulated by SS within Each Age Group

In our shape-matching design, we parametrically varied structural similarity to identify brain regions involved in processing structural descriptions. Using cross-correlation analysis, we isolated the regions more sensitive to high SS and low SS in each age group. From all age groups, a total of forty-eight possible regions indicating sensitivity to SS, known as regions of interest (ROIs), were identified; twenty ROIs in 5-8 year olds, fourteen ROIs in 9-11 year olds, and fourteen in adults.

To verify the effect of SS on fMRI signal, we submitted each ROI to a one-way repeated measures ANOVA with SS Level (percentage signal change = (SS level –baseline)/baseline) as the within-subject factor. Twenty-one of the forty-eight clusters survived as significant at $\underline{p}<.05$ or significant at $\underline{p}<.09$ for the effect of SS level on signal magnitude including seventeen linear (systematic) and four non-linear (non-systematic) functions. Here, we focused on regions with only linear changes in signal magnitude. Tables 1 and 2 identify the fourteen ROIs sensitive to high SS and the three ROIs sensitive to low SS respectively. None of the three clusters sensitive to decreasing SS were within the VPS. For regions sensitive to increasing SS, only five fell within the VPS and only four of those were linear increases (see Table 5.1).

Four of the VPS clusters in this study were similar to regions previously identified as sensitive to high SS (for either shape or animal stimulus pairs) in adults (Joseph & Gathers, 2003). Within the 9-11 year old group, we found one right fusiform cluster (x = 44, y = -64, z = -14) and one left mid-anterior fusiform locus (x = -53, y = -45, z = -29) sensitive to high SS. The left fusiform cluster occurred just lateral to that of a previously identified left mid-fusiform (x = -37, y = -49, z = -24) site sensitive to high SS in adults for an animal-matching task (Joseph & Gathers, 2003). In the current adult group, one left mid-anterior fusiform region (x = -50, y = -58, z = -20) appeared that was comparable to the 9-11 year old fusiform site and to a previously identified SS region (Joseph & Gathers, 2003). Our results also indicated a previously identified posterior region modulated by SS in the right inferior occipital gyrus region (x = 37, y = -81, z = 3). In addition, a posterior left fusiform region (x = -47, y = -72, z = -18) lateral to a previous shape-sensitive region (Joseph & Gathers, 2003) was significant for the effect of SS; however, it did not have a linear function.

In general, the number of structurally modulated clusters within the VPS increased with age. Five to eight year olds had no shape-sensitive VPS clusters whereas 9-11 year olds and adults had VPS clusters sensitive to high SS processing. The VPS clusters found in 9-11 year olds and adults were similar to clusters from other adult structural similarity studies (Joseph & Gathers, 2003). From these results, it appears that structurally sensitive object processing in the VPS develops after 5-8 years of age. Furthermore, based on the absence of VPS clusters sensitive to low SS at all ages, the VPS plays a role in high SS processing rather than low SS processing with maturation.

Other Regions Modulated by SS within Each Age Group

Based on previous reports that visual processing recruits networks throughout the cortex (Gathers & Joseph, 2003a; Joseph & Farley, 2004; Joseph & Gathers, 2003), we expected to find cortical areas outside of the VPS (e.g. frontal and parietal regions sensitive to high SS) involved in SS processing in children and adults. In addition, from other findings (Chapter 6), we predicted developmental changes in extra-VPS regions with children activating more clusters beyond the VPS than adults. Again, we report only regions with statistically significant linear increases or decreases in fMRI signal as a function of SS level.

Three ROI’s from the 5-8 year old group, two frontal regions sensitive to high SS and one cerebellar region sensitive to low SS, survived the one-way ANOVA. Of the five 9-11 year old clusters that survived the one-way ANOVA, all were significant for high SS and were located in frontal and parietal regions. Analysis of adult shape sensitivity in other cortical regions revealed two right hemisphere ROIs sensitive to high SS, one superior frontal and one superior parietal cluster. Adults also produced two left ROIs significant to low SS, a left cerebellar region and a left superior frontal region. In general, frontal activation sensitive to high SS was significant within each age group. However, parietal activation was specific to 9-11 year olds and adults. Furthermore, adult clusters beyond the VPS followed a pattern of lateralization with all high SS sensitive regions in the right hemisphere and all low SS sensitive regions in the left hemisphere. For 5-8 year olds and adults, low SS activity occurred in cerebellar regions, though in different hemispheres.

Developmental Changes in Structurally-sensitive Regions

To clarify the developmental roles of the seventeen ROIs significant for a linear main effect of SS level, we performed mixed repeated-measures ANOVAs with SS level (SS1 to SS3) as the within-subject factor and Age (5-8 year olds, 9-11 year olds, and adults) as the between-subjects factor. As seen in Tables 5.1a and 5.2a, our mixed ANOVAs yielded four ROIs with significant ($\underline{p}<.05$) or marginally significant ($\underline{p}<.09$) main effects of age, five ROIs with significant or marginally significant main effects of SS level, and seven ROIs with significant or marginally significant SS Level x Age interactions. Based on other developmental data from our lab (Gathers, Bhatt, Corbly et al., 2004) [Chapter 4; see Chapter 6], we expected to find regions in which signal was a function of age and regions in which signal was a function of SS level (Joseph & Gathers, 2003). For the purpose of this study, however, we focused on clusters with significant SS level x Age interactions (see Tables 5.1, 5.2, and 5.3) to assess developmental changes in neural correlates for structural similarity. Simple main effects of SS at each age level were performed on clusters with significant SS level x Age interactions. In general, we found seven cortical regions associated with maturational changes in structural processing, two within the right VPS -- one mid-fusiform locus ($\underline{p}<.064$) and one inferior occipital locus ($\underline{p}<.056$). See Figure 5.6. In all but one cluster significant for the interaction of SS level x Age, significant or marginally significant simple main effects of SS were found for older children indicating a shift in SS processing between 9-11 years of age.

Beyond the VPS, a maturational pattern emerged in which both groups of children used frontal regions and older children used parietal regions for high SS discrimination (Figure 5.7). Discrimination of low SS occurred in posterior cerebellar areas for older children and adults. All surviving frontal and parietal clusters were sensitive to increasing structural similarity. Three frontal regions survived the between-groups analysis with significance for the interaction of SS level x Age including one left superior frontal region (x = -7, y = 14, z = 68) and two right hemisphere clusters (middle and inferior frontal) [$F(4,60) = 2.6$, $\underline{p}<.046$; $F(4,60) = 3.3$, $\underline{p}<.016$].

Overall, we found age-related changes in functional activation patterns for structural processing in the VPS and other cortical regions. One VPS and five non-VPS regions showed significant or marginally significant simple main effects of SS in older children suggesting a maturational shift in structural processing around 9-11 years of age. In addition, cortical shifts occur in SS processing with frontal and parietal regions used for high SS processing in childhood and cerebellar regions active in processing low SS in adults.

Face-Sensitive VPS Regions Modulated by SS

In addition to identifying SS responsive areas, we used a passive face and object viewing task to isolate face sensitive (face-preferential) regions in each group. As in previous analyses (Gathers, Bhatt, Corbly et al., 2004; Joseph & Gathers, 2002), we distinguished face preferential regions as areas in which faces produced a statistically greater response than other non-face object stimuli and baseline. Face-preferential regions were isolated based on reports in other studies of a face processing VPS region (e.g. the fusiform face area) (Kanwisher et al., 1997). A goal of this study was to investigate development and function of the FFA in regards to structural processing. Therefore, we limited our face preferential analyses to the ventral processing stream.

Following cluster isolation, one-way repeated measures ANOVAs and post-hoc t-tests were conducted to verify face-preferential profiles. Under these criteria, only three adult face-preferential regions survived. Neither child group produced VPS face-preferential clusters that withstood the ANOVA and subsequent post-hoc t-tests. In adults, posterior VPS face-preferential clusters occurred bilaterally including clusters in the fusiform and lingual gyri. A left posterior fusiform (x = -32, y = -77, z = 14) cluster corresponded with previously reported face-preferential regions isolated in adults (Joseph & Gathers, 2002). Overlay results of face-preferential and structurally-sensitive regions revealed no significant shared regions within the VPS for these posterior adult clusters. In children 9-11 years of age, face-preferential activation and high SS responses shared a mid-fusiform region (x = 46, y = -60, x = -18) similar to a previously identified face sensitive region in the same age group (Gathers, Bhatt, Corbly et al., 2004). However, this region of overlap did not survive the one-way ANOVA and post-hoc t-tests for the face-preferential profile. Thus, in these analyses, sensitivity to high SS did not provide a mechanistic explanation for face processing in children or adults.

Discussion

In our current analyses, we explored the idea of a structural similarity mechanism as the basis for visual object recognition across development. Our two primary objectives were: (1) to identify developmental changes in the behavioral and functional correlates of structural similarity processing in children 5-8 years, 9-11 years, and adults and (2) to investigate the possibility of a structural mechanistic basis for face-sensitive processing regions (FFA) in development.

Behavioral Evidence of Developmental Changes in SS Processing

In general, behavioral measures indicate that similar to adults, children use a structural similarity mechanism for shape processing. Measures of error rates and sensitivity reflect a direct influence of structural manipulation on behavior in both children and adults. However, fMRI activation indicates developmental changes in the neural correlates of structural similarity processing from 5 years to adulthood. The apparent disparity of error and sensitivity measures with fMRI measures in regards to mechanistic and functional evidence of developmental changes in SS processing may be explained by measures of bias. Though children and adults both use SS processing, the strongly liberal bias of adults at SS3 compared to both groups of children indicates that adults may employ a different criterion setting for processing highly similar shapes than children. Thus, our fMRI measures in conjunction with our bias measures imply maturational changes in structural similarity processing that may be contributed to age-related changes in strategy. Maturational changes in strategies involving visual processing are not unfamiliar. Using feature and conjunction search tasks and an object classification task, Ruskin and Kaye investigated developmental changes in object processing in three groups of children: ages 5-6 years, 7-8 years, and 11-12 years (Ruskin & Kaye, 1990). Their results indicated that developmental differences in processing efficiency led younger subjects to use a different visual classification strategy than 11-12 year olds.

Some might argue that our results reflect design differences rather than maturational changes. In our current study, stimulus presentations did differ for adults (400ms) and children (1500 ms) with total possible response times of (2000ms) and (3000ms) respectively. However, other data from our lab imply stimulus duration does not affect findings related to SS processing. In an unpublished animal-matching study, we tested adults on four levels of SS and three levels of exposure duration (200, 400, or 1900 ms). We found that exposure duration did not alter the reaction times or error rates associated with SS. In a similar published work, behavioral trends in the main effect of SS for RT and sensitivity were preserved at multiple durations (Joseph & Farley, 2004). Furthermore, in a developmental behavioral study in which experimental designs were equivalent between age groups (stimulus durations were 2500 ms followed by 500ms fixations), we again found strategic differences in adults and children (Gathers, Bhatt, & Joseph, 2004). In this same/different matching study where SS was parametrically varied for animal (object) and face stimuli, 6-8 year old children and adults had similar criterion setting for faces but not for animals. For animals, children were more conservative relative to faces and adults were more liberal. Hence, our current findings are not attributed to design discrepancies but reflect true developmental changes in SS processing linked to age-related changes in criterion settings.

Evidence of Developmental Changes in SS Processing in the VPS

Our current imaging analyses reveal unique patterns of structurally significant neural activity for 5-8 year olds, 9-11 year olds, and adults. Younger children produce no significant SS activation in the VPS. However, for older children (9-11 years) and adults, bilateral ventral processing stream regions are sensitive to high structural similarity. Though older children activate more anterior VPS regions relative to adults, both groups have a similar pattern of activation. Older children and adults have functional regions in the VPS sensitive to high SS object processing whereas younger children show no functional differentiation for SS in the VPS. These findings agree with face recognition data indicating more adult-like visual processing by 10 years of age (Carey & Diamond, 1994).

At first, our results seem to contradict other developmental object processing studies that report shape processing from infancy to adulthood. For example, in an object categorization study, Ward (1989) found that five year old children demonstrated predominately analytical or piece-meal processing of non-face stimuli similar to adults. In light of this and other reports that present evidence of structural mechanisms as early as infancy (Bertin & Bhatt, 2001; Bhatt et al., 1999; Bhatt & Waters, 1998; Quinn et al., 2001), one might predict no developmental differences in structural object processing. However, as mentioned previously, though even newborns are sensitive to shape, other studies indicate that children and adults use different shape recognition strategies (Abecassis et al., 2001; Gershkoff-Stowe & Smith, 2004; Gibson et al., 1962; Landau et al., 1998; Piaget & Inhelder, 1948; Smith, 2003). Recent studies have shown that object recognition involves some aspect of relational processing in addition to analytical processing (Davidoff & Roberson, 2002; de Gelder & Rouw, 2000b; Reed et al., 2003). If object recognition involves relational processing to some degree and if relational processing develops with age (Carey & Diamond, 1994; Freire & Lee, 2001; Freire & Lee, 2003a; C. J. Mondloch et al., 2003; Mondloch et al., 2002; Schwarzer, 2000) or experience (see Diamond & Carey, 1986; Gauthier & Tarr, 1997; Rhodes, Brennan, & Carey, 1987) then our findings of developmental changes in structural similarity processing are potentially related to changes in relational processing (Piaget & Inhelder, 1948).

Though the interpretation of our findings may be arguable, our study is not the first to reveal developmental changes in the functional organization of the VPS. Another developmental fMRI study confirmed age-related changes in the functional neural correlates of visual recognition (Aylward et al., 2005). Aylward et al. (2005) examined activation patterns in the fusiform gyrus for two groups of children (younger, 8-10 years and older, 12-14 years) viewing two categories of stimuli, faces and houses. In the older children, faces produced a significantly greater response than houses in the bilateral fusiform gyri. This differential response was absent in the younger children. Aylward interpreted the results to suggest an increase in categorical differentiation with age. In light of our current findings however, we propose that the greater fMRI response by faces than houses in the fusiform gyrus of 12-14 year olds may be attributed to a maturational increase in sensitivity to structural similarity rather than to taxonomic category. The idea of structurally-driven developmental changes in face processing forms the basis for our second objective (see discussion section *The Role of Structurally Similarity in Face Processing*).

One could dispute that the lack of VPS regions responsive to SS in younger children is due to thresholding and signal magnitude differences among age groups (Gaillard et al., 2000). Though no structurally-sensitive regions appeared in the VPS of 5-8 year olds, a left superior frontal region sensitive to high SS was significant (Figure 5.7). Furthermore, as seen in Figure 5.7, the signal magnitude for younger children is sometimes greater than that of older children and adults. Thus, thresholding is not an explanation for absence of structurally sensitive VPS regions in 5-8 year olds. Our fMRI results appear to reflect true developmental changes in structural processing from five years of age to adulthood.

Potential Hemispheric Roles in SS Processing and Maturation

Data from both older children and adults revealed bilateral activity for high SS stimulus pairs. Per evaluation of their Talairach coordinates, these SS sensitive VPS regions are in the proximity of the lateral occipital complex (LOC), an area known to function in shape recognition (Grill-Spector, Kushnir, Edelman, Itzchak, & Malach, 1998; Grill-Spector, Kushnir, Hendler et al., 1998; Kourtzi & Kanwisher, 2000; Malach et al., 1995; Whatmough, Chertkow, Murtha, & Hanratty, 2002). The LOC has been consistently identified bilaterally, but the different hemispheric roles of the LOC in the discrimination of highly similar shapes are unknown. Here we speculate as to the contribution of each hemisphere in SS processing.

We found left mid-fusiform regions in 9-11 year olds and adults that were consistent with shape-sensitive regions identified in our former structural similarity investigations (Joseph & Farley, 2004; Joseph & Gathers, 2003). Two right hemisphere VPS clusters were also identified, one mid-anterior fusiform and one inferior occipital. In our previous study, the orientation of objects in the stimulus pairs varied (Joseph & Gathers, 2003), therefore we proposed that the left hemisphere might be responsible for processing viewpoint-invariant object representations (Vuilleumier, Henson, Driver, & Dolan, 2002) and the right hemisphere might be involved in processing viewpoint-dependent representations. Because the current stimuli are the same as those used in Joseph & Gathers (2003) the explanation of differential hemispheric processing of viewpoints may still apply.

As an alternative, left hemisphere and right hemisphere involvement may be indicative of knowledge type and difficulty imposed by the task respectively. In a positron emission tomography (PET) study, Moore and Price (1999) used naming and matching tasks to differentiate among functional correlates for object categorization (semantics), object configuration, and object identification. The authors compared functional patterns produced by contrasts of simple-shaped or multi-component natural, man-made, and non-object stimuli. Neuroimaging results indicated left occipito-temporal cortex involvement was based on knowledge type (perceptual and functional) with more anterior regions activated by perceptual judgments and more posterior regions activated by functional judgments. In contrast, right hemisphere activation reflected structural task demands. Natural objects, with more structural similarities than the other stimulus categories tested, produced anterior and posterior temporal activation in the right hemisphere while other stimulus categories activated the right postcentral gyrus. We apply the findings of Moore and Price to our current analyses. Because our stimuli are basic shapes rich in perceptual but poor in functional information, we speculate that left mid-anterior fusiform activation by highly similar geon pairs is due to task reliance on perceptual knowledge.

Further support for right hemisphere involvement in structural processing demands comes from studies by Gerlach and colleagues (Gerlach, Law, Gade, & Paulson, 1999; Gerlach et al., 2004). Using PET, Gerlach et al. found that activity within the right posterior inferior temporal gyrus corresponded with degrees of perceptual differentiation required for recognition (1999). And in a later study, Gerlach and colleagues report right hemisphere activation in difficult object decision tasks requiring more fine-grained perceptual differentiation (2004). Thus, greater processing demands evoked by discrimination of high SS may explain findings of right hemisphere VPS activity in the present data.

A final explanation of hemispheric involvement in SS processing relates directly to maturation. Our analyses indicated maturational changes in SS processing in the right VPS. In particular, between group analyses revealed a significant interaction of SS Level x Age for the right mid-fusiform and right inferior occipital gyri. The location of this cluster corresponds to a previously identified right hemisphere locus sensitive to relational (holistic) processing (Lerner et al., 2001). Based on the current findings, we suggest that age-related hemispheric lateralization for SS processing reflects developmental changes in featural and relational processing.

Several studies provide support for this reasoning. In a behavioral study, Mondloch et al. (2003) reported that the processing of hierarchical geometric shapes continues to develop into adolescence. They found slower development of relational processing (i.e. local/configural processing based on high spatial frequencies) than general global shape processing. In particular, adult-like relational processing developed between 10-14 years of age and was localized to the right hemisphere as evidenced by visual field testing. Mondloch and colleagues' findings of a right hemisphere bias for relational processing correspond to fMRI findings in adults (Martinez et al., 1997) and children (Moses et al., 2002). In a developmental fMRI study of relational (global) versus featural (local) processing, Moses and colleagues imaged children ages 12-14 years and then categorized them as bilateral immature or mature lateralized based on their response time profiles (Moses et al., 2002). The immature bilateral group produced greater activation overall to features (local), similar response patterns bilaterally to relational (global) conditions, and a trend of right hemisphere activation greater than left for local features. The mature lateralized children demonstrated adult-like activation patterns with greater right hemisphere activation during relational (global) processing and greater left hemisphere activity in response to local featural processing. Based on these studies, we suggest that the role of the right hemisphere in our SS processing task corresponds with findings of developmental changes in featural and relational processing strategies.

None of our speculations of hemispheric roles in SS processing is necessarily mutually exclusive. The effect of viewpoint processing may be tightly linked to task demands (Lawson, 2004) and task knowledge requirements. In the same way, task demands may be tightly linked to processing strategies (Shedden & Reid, 2001). Thus, all three accounts for bilateral hemispheric activation in structural processing are possible explanations for our present findings.

Other Cortical Regions

Previous data support the existence and maturation of structural processing regions beyond the VPS (Gerlach et al., 2004; Joseph & Farley, 2004; Joseph & Gathers, 2003). In the present analyses, we found age-related changes in the functional correlates of structural similarity processing in five non-VPS regions. From these non-VPS regions, two patterns emerged. First, significant or marginally significant simple main effects in older children were common to all five regions suggesting a maturational shift in structural processing between 9-11 years of age. As noted in our discussion of present VPS findings, other studies support similar ages for developmental changes in visual processing (Carey & Diamond, 1994; Schwarzer, 2000).

Second, a general anterior to posterior shift in SS processing occurs in development. Children recruited primarily frontal and parietal regions with systematically stronger activation for high SS processing most prevalent in older children. In contrast, a posterior cerebellar region, involved in low SS processing, was increasingly active from age 9 years to adulthood. Other studies note recruitment of frontal and parietal regions in object recognition tasks involving structural similarity processing (Gerlach et al., 2004; Joseph & Farley, 2004; Joseph & Gathers, 2003). In a review, Kanwisher and Wojciulik note that “attention is central to the construction of every visual experience” explaining that fronto-parietal networks may aid in directing visual attention to spatial locations, features, or whole objects (Kanwisher & Wojciulik, 2000). Frontal and parietal involvement may relate to top-down attentional influences in visual processing (Joseph & Farley, 2004; Joseph & Gathers, 2003; Kanwisher & Wojciulik, 2000; Mondloch et al., 2003). The parietal lobe is active in a variety of attentional tasks (Kanwisher & Wojciulik, 2000), one of which is allocation (Robertson & Lamb, 1991). As SS processing demands increase, children may have more difficulty than adults allocating more of their attention or selectively attending to significant stimulus differences (Gibson, 1969). Less control over the allocation of their attention and yet greater demands on their need to selectively attend with increasing SS levels may result in stronger recruitment of the fronto-parietal network in children than adults. As implied by behavioral shifts in bias and hemispheric shifts in SS processing with age, developmental changes in SS processing strategies may account for fronto-parietal activation in children.

Overall, the finding that frontal and parietal regions are linked to developmental changes in SS processing is consistent with knowledge of neural development. Though 9-11 year olds continue to use a conservative strategy like younger children, their fMRI patterns are most similar to adults. This apparent transition in SS processing may be due to corresponding changes in neural architecture (see Chapter 6).

The Role of Structural Similarity in Face Processing

Considering the homogeneity of faces in their first order configurations (i.e. eyes above nose, nose above mouth), external shape, and general features, face recognition requires a great deal of discrimination to delineate subtle differences in features and inter-featural relationships. Thus, we hypothesized that the mechanistic basis of face recognition was structural similarity processing. Because faces are highly similar to one another, a structural basis for face processing would be evidenced by co-localized regions of high structural similarity processing and face-preferential responses. In addition, we hypothesized a developmental change in the mechanistic basis of face processing. Our developmental hypothesis was based on a compilation of data from multiple face and object processing studies. Results from many researchers indicate developmental changes in face processing (Carey & Diamond, 1994; Freire & Lee, 2001; Freire & Lee, 2003b; Mondloch et al., 2002; Mondloch et al., 2003; Schwarzer, 2000).

At the group level, we found no VPS regions of co-localization at any age for face-preferential and SS responses. Therefore, our current data do not directly support our hypothesis that face processing is based on a structural similarity mechanism. However, the possibility cannot be ruled out. An explanation for the lack of overlap in SS processing in 3-D shapes and face processing in our subjects may be based on task design rather than the absence of SS processing in face recognition.

It is known that face-preferential regions (i.e. FFA) and shape sensitive regions (i.e. LOC), particularly those sensitive to high shape similarity (Joseph & Gathers, 2003; Price, Noppeney et al., 2003), are located near each other in the mid-anterior fusiform gyrus (Grill-Spector, Kourtzi, & Kanwisher, 2001). In fact, partial overlap of the two regions is reported (Grill-Spector et al., 2001). The LOC may represent a continuum of shape processing with more and more anterior regions specialized for greater degrees of shape similarity (Lerner et al., 2001; Price, Noppeney et al., 2003). As faces represent the extreme end of the continuum of shape processing (Bruce & Humphreys, 1994), traditional face regions (i.e. the FFA, Kanwisher et al., 1997), near but more anterior to shape regions, may be drawing on even more distinct structural processing. For example, Lerner et al. examined fMRI signal changes in the VPS in response to parametric manipulations of featural and relational (i.e. holistic) representations of cars and faces (2001). Responses to car and face stimuli did not overlap spatially; however, results indicated an increasing sensitivity to relational (i.e. holistic) representations in increasingly anterior regions of the VPS for both stimuli. From Lerner and colleagues findings, we infer that structural similarity processing of stimuli may include degrees of featural and holistic processing with faces requiring a greater degree of relational (holistic) differentiation than that of cars or, in our case, geometrical shapes (2001). Thus, absence of spatial overlap between regions sensitive to high structural similarity and regions sensitive to faces may be the result of a task design in which we only manipulated structural similarity of objects (3-D shapes).

Table 5.1 VPS Areas Sensitivity to High Structural Similarity

region	BA	Taliarach (x,y,z)	Cluster size (voxels)	Mixed ANOVA		
				SS Effect	Age	SS x Age
R. FG	37	44, -64, -14	48		$F(2,30) = 3.3$, $p < .052$	$F(4,60) = 2.6$, $p < .064$
R. IOG	37	37, -81, -3	18			$F(4,60) = 2.6$, $p < .056$
L. FG	19	-53, -45, -29	21		$F(2,30) = 3.5$, $p < .045$	
L. FG	19	-50, -58, -20		$F(2,60) = 2.6$, $p < .086$		

Note. VPS, ventral processing stream; R, right; L, left; FG, fusiform gyrus; IOG, inferior occipital gyrus; BA, Brodmann’s area; x, medial-lateral coordinate; y, anterior-posterior coordinate; z, inferior-superior coordinate; SS, structural similarity.

Table 5.2 Other Cortical Areas Sensitivity to High Structural Similarity

region	BA	Taliarach	Cluster size	Mixed ANOVA		
		(x,y,z)	(voxels)	SS Effect	Age	SS x Age
L. SFG	6	-7, 14, 68	86	F(2,29) = 3.2, p < .057		F(4,58) = 3.1, p < .021
R. MFG	9	49, 7, 37	24	F(2,60) = 2.6, p < .080		F(4,60) = 2.6, p < .046
R. IFG	11	27, 5, -21	67			F(4,60) = 3.3, p < .016
L. IPL	40	-29, -52, 44	44		F(2,30) = 6.4, p < .005	
R. MFG	47	13, 21, -21	113			
L. MFG	46	-48, 44, 20	36	F(2,60) = 5.8, p < .005		
R. SPL	7	25, -57, 55	54		F(2,30) = 2.8, p < .078	
R. SFG	10	14, 70, 3	15			
R. SPL	7	30, -70, 31	18			
R. Precuneus	19/7	29, -59, 38	59		F(2,30) = 3.4, p < .048	

Note. R, right; L, left; SFG, superior frontal gyrus; IFG, inferior frontal gyrus; IPL, inferior parietal lobule; MFG, middle frontal gyrus; SPL, superior parietal lobule; BA, Brodmann's area; x, medial-lateral coordinate; y, anterior-posterior coordinate; z, inferior-superior coordinate; SS, structural similarity.

Table 5.3 Areas Sensitive to Low Structural Similarity

region	BA	Taliarach (x,y,z)	Cluster size (voxels)	Mixed ANOVA SS Effect	Age	SS x Age
L. Cerebellum		-30, -49, -21	22	F(2,18) = 5.2, $p < .024$	F(2,60) = 3.0, $p < .059$	F(4,60) = 3.1, $p < .023$
R. Cerebellum		40, -55, -30	74	F(2,18) = 9.4, $p < .008$		
L. SFG	9	-25, 33, 31	13	F(2,18) = 6.5, $p < .013$		

Note. L, left; R, right; SFG, superior frontal gyrus; BA, Brodmann's area; x, medial-lateral coordinate; y, anterior-posterior coordinate; z, inferior-superior coordinate; SS, structural similarity.

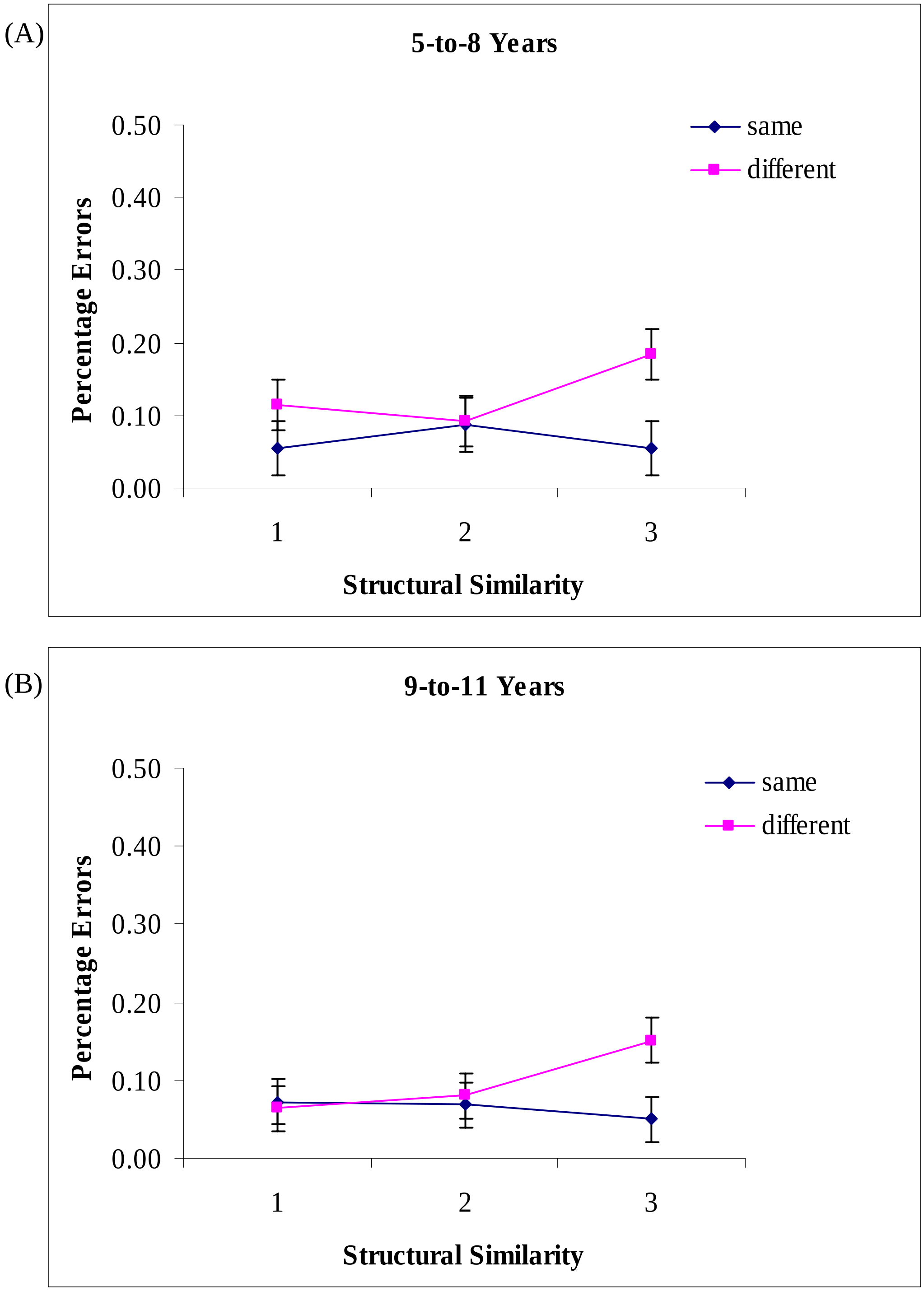


Figure 5.1. Child Error Rates (RT). Average error rates for "yes" and "no" responses in (A) 5-8 year olds and (B) 9-11 year olds. Error bars represent within-group confidence intervals.

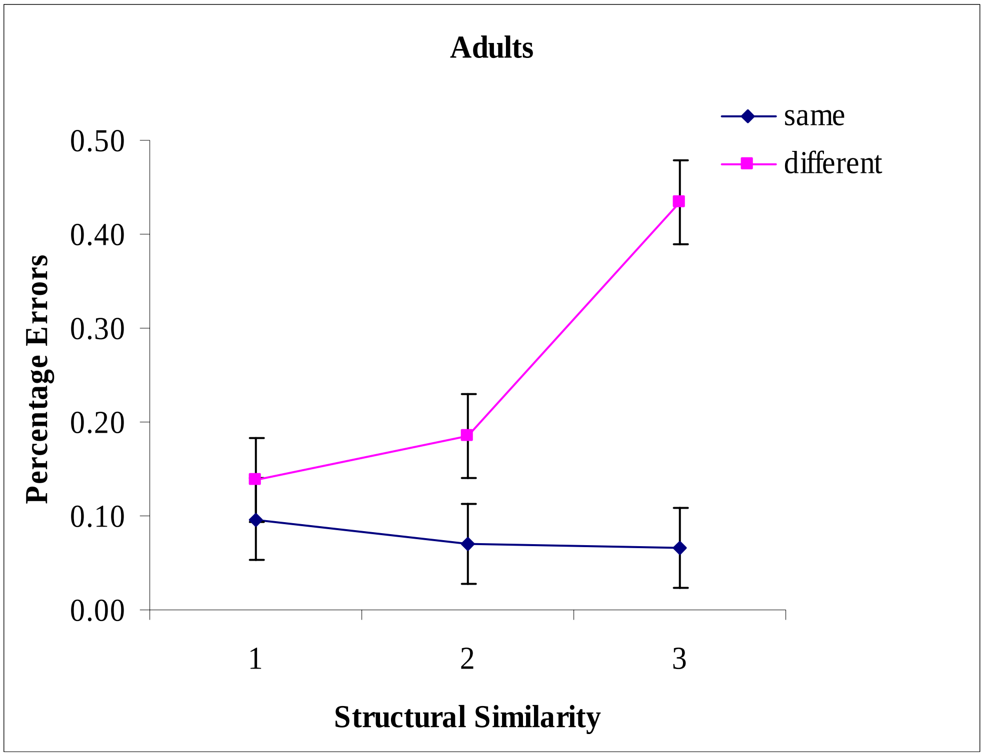


Figure 5.2. Adult Error Rates (RT). Average error rates for “yes” and “no” responses in adults. Error bars represent within-group confidence intervals.

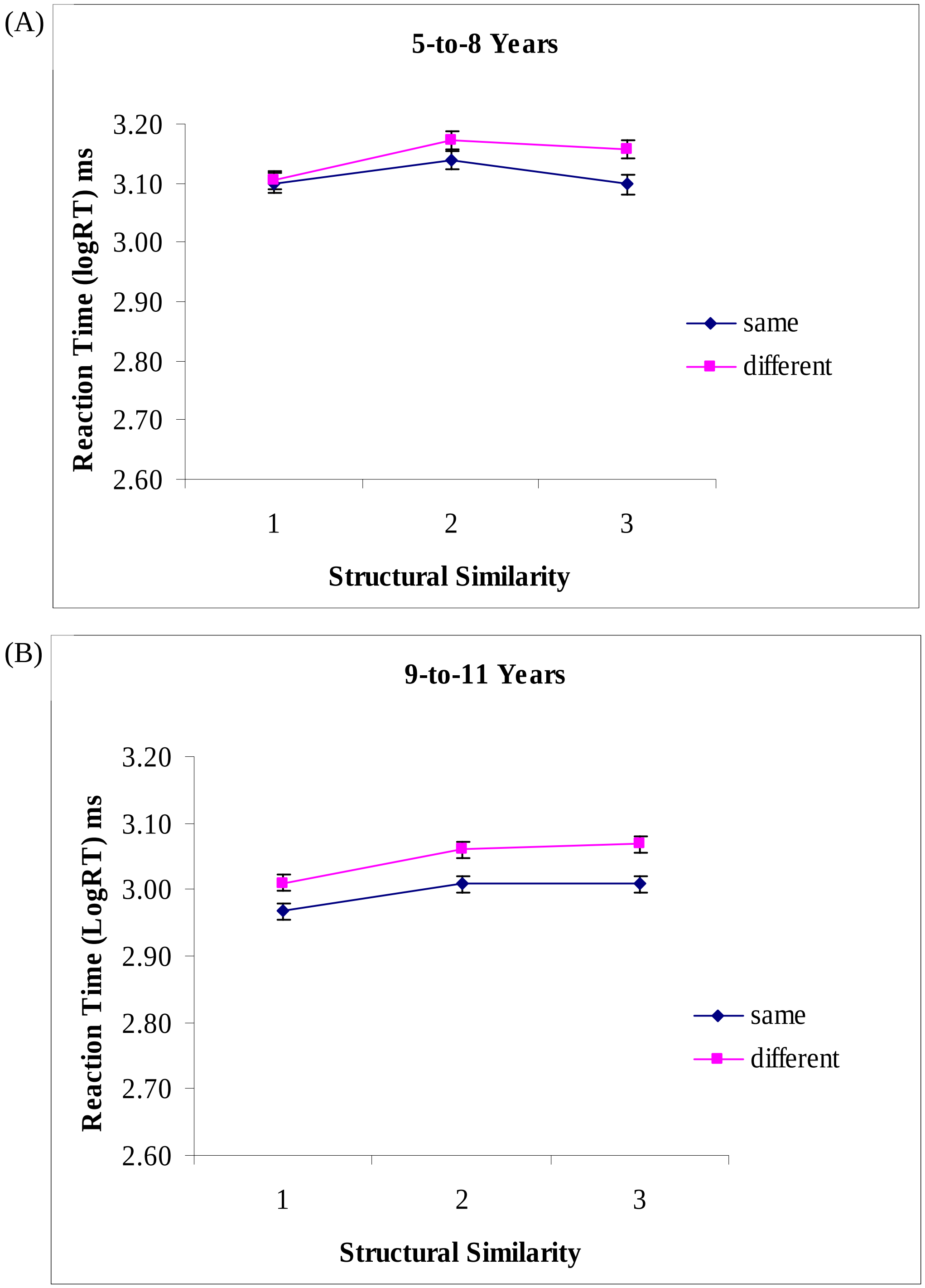


Figure 5.3. Child Reaction Times (RT). Average RT for “yes” and “no” responses in (A) 5-8 year olds and (B) 9-11 year olds. Error bars represent within-group confidence intervals.

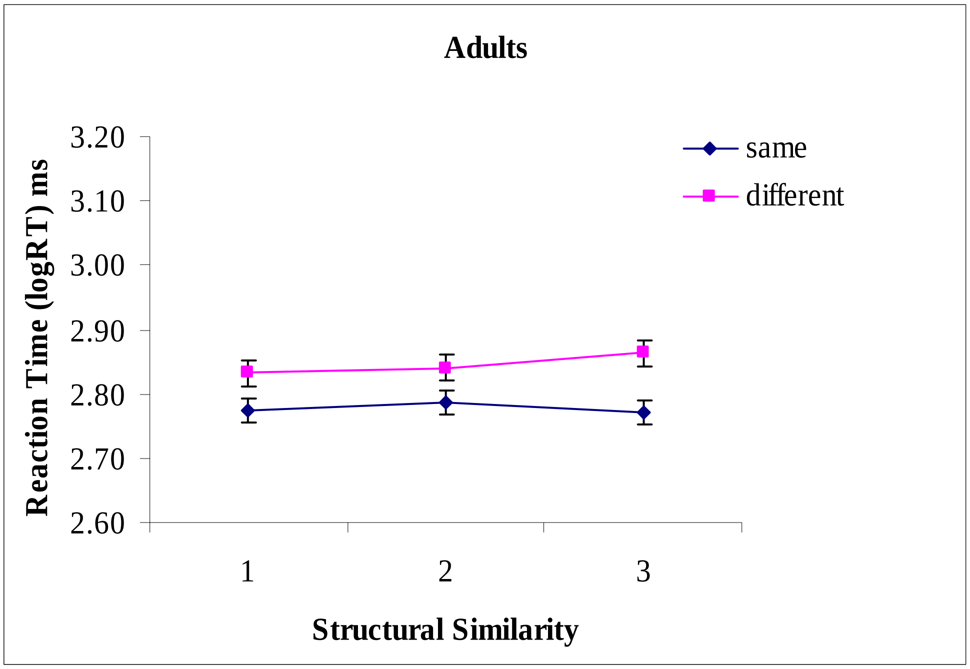


Figure 5.4. Adult Reaction Times (RT). Average RT for “yes” and “no” responses in adults. Error bars represent within-group confidence intervals.

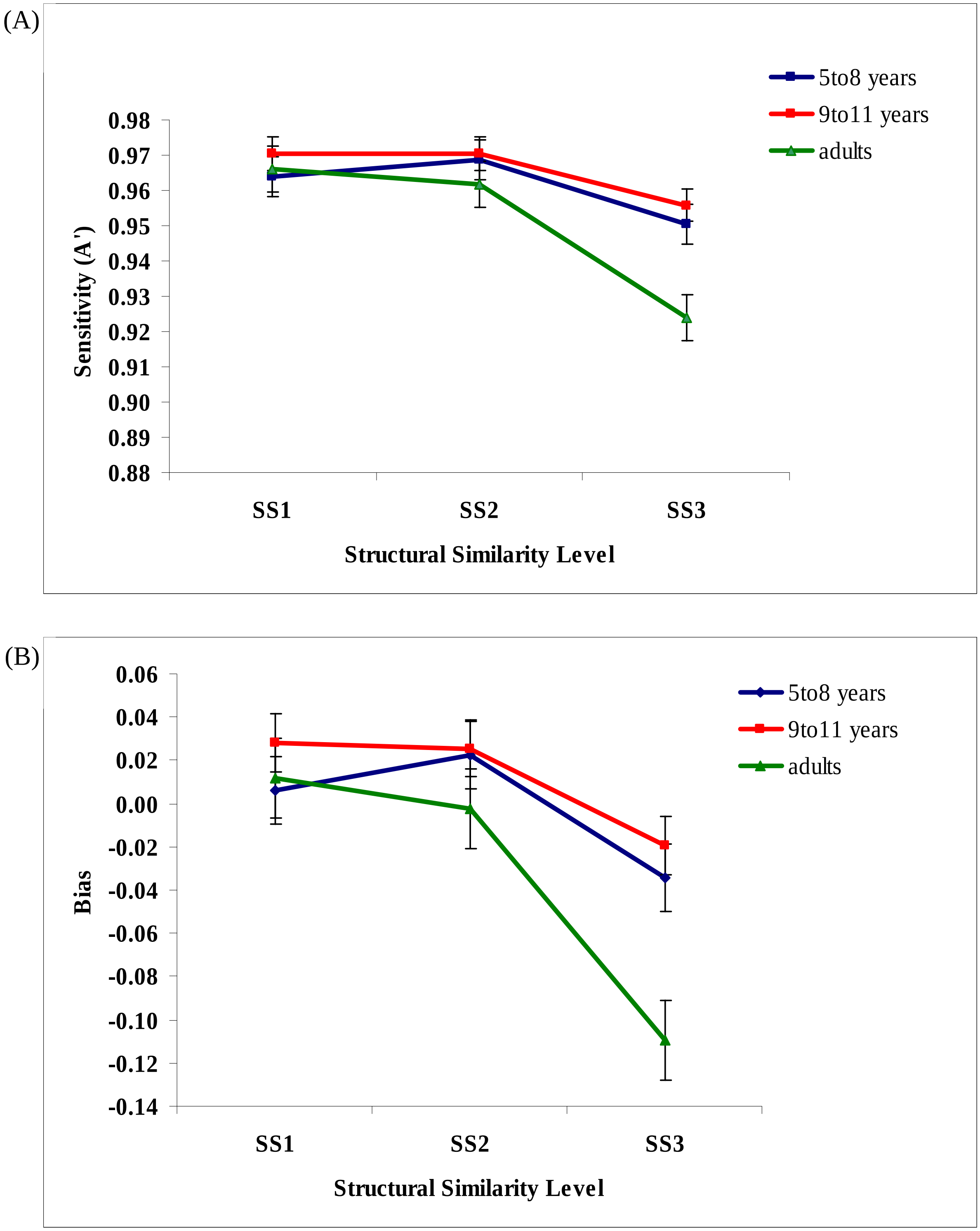


Figure 5.5. (A) Sensitivity and (B) bias results for the shape-matching task. Error bars reflect within-participants confidence intervals.

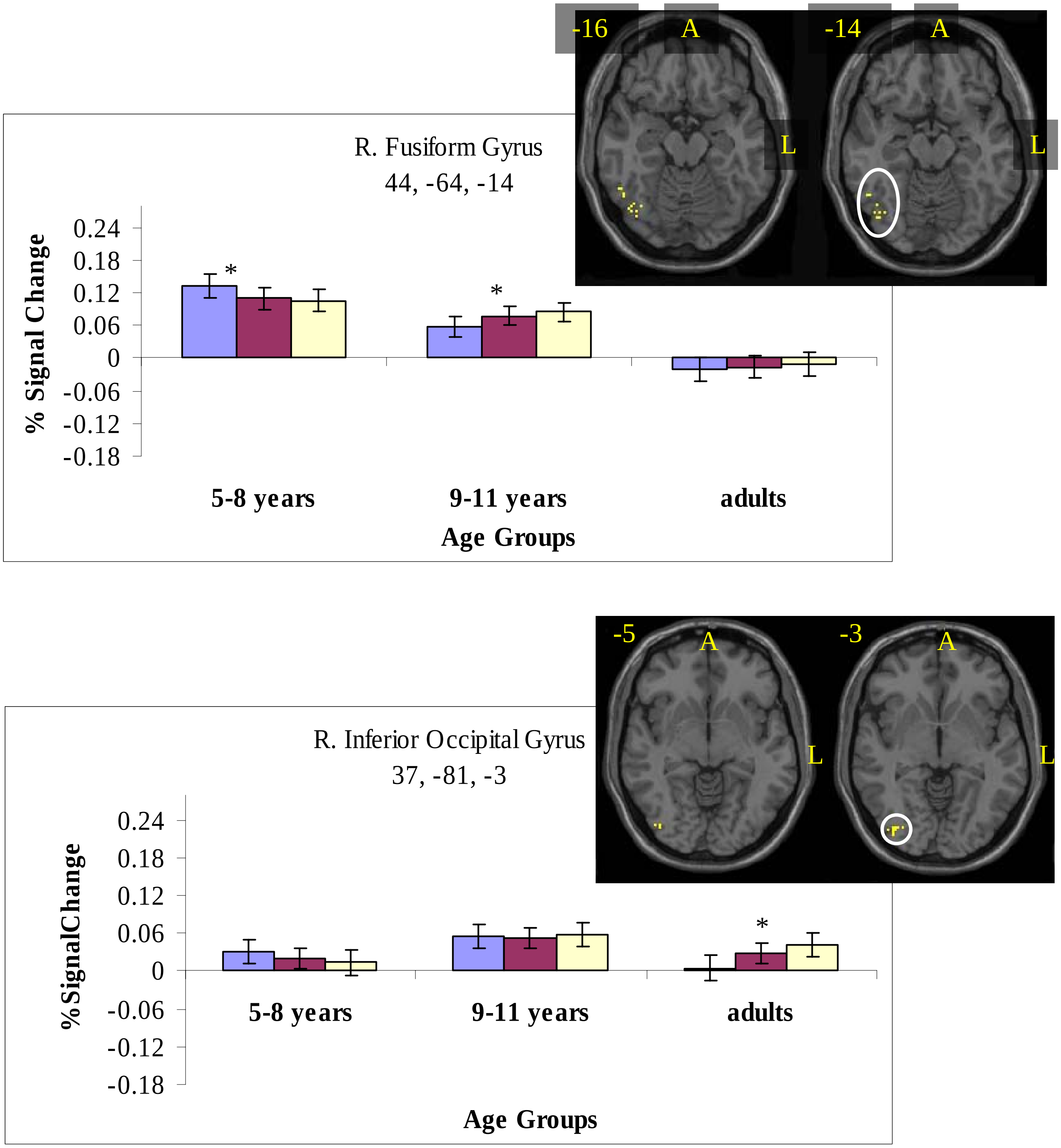


Figure 5.6. Ventral processing stream (VPS) regions modulated by maturational changes in structural similarity (SS). * Indicates significant simple effect of SS. Error bars represent within-group confidence intervals. R = right, L = left, A = anterior. Taliarach z coordinates in left, top corner of functional images indicate mm inferior to a plane through the anterior and posterior commissures.

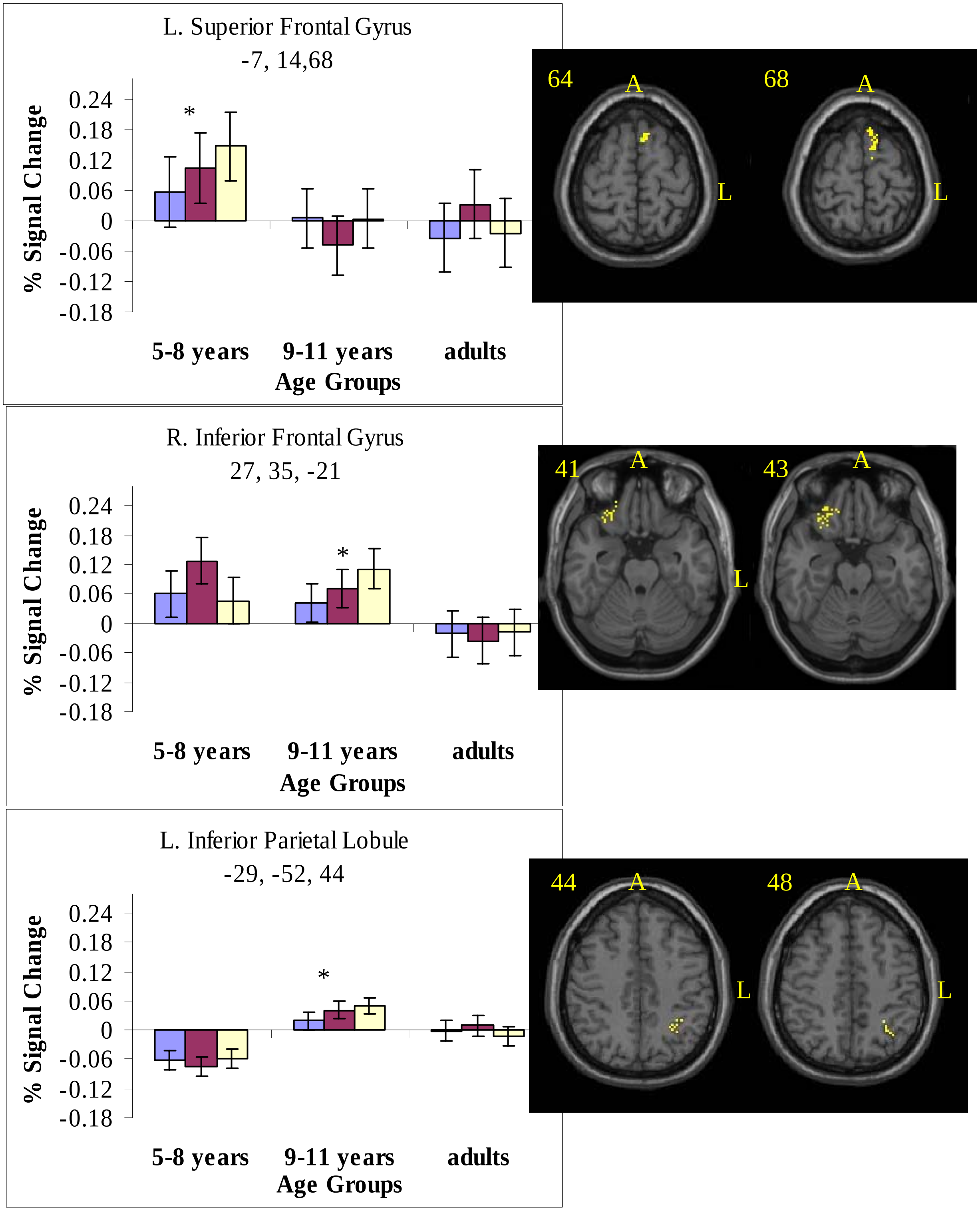


Figure 5.7. Frontal and parietal regions modulated by maturational changes in structural similarity (SS). * Indicates significant simple effect of SS. Error bars represent within-group confidence intervals. R = right, L = left, A = anterior. Taliarach z coordinates in top left indicate mm inferior to a plane through the anterior and posterior commissures.

Chapter Six: Developmental changes in fMRI measures of activation extent, signal magnitude, and lateralization for face and object processing from five years to adulthood

Summary

The current analyses expand upon existing work by assessing changes in face and object processing in the entire cortex, using measures of extent, magnitude, and lateralization of activation at both global and local levels, and characterizing network-wide changes in activation profiles. Children recruited a greater number of smaller regions for face and object processing whereas adults recruited fewer but larger regions of activity. However, contrary to current predictions in literature of increased functional selectivity with maturation (Aylward et al., 2005; Passarotti et al., 2003), these developmental changes in extent occurred only for regions of shared object and face processing (i.e. conjoined). Overall fMRI signal strength did not change systematically across age groups, but regional progressions and regressions of signal reflected developmental network changes. Not specific to stimulus category, signal strength decreased with age for frontal regions but increased for age in parietal and VPS regions. Furthermore, children produced primarily bilateral activation whereas adult brain activity was lateralized to the right. As with measures of activation extent and signal magnitude, hemispheric changes were not category-specific. A narrowing of face and object processing networks does occur with age, which may correspond with underlying neuroanatomical changes and/or functional changes related to task rather than categorical processing.

Introduction

In this chapter, we reevaluate data (Gathers, Bhatt, Corbly et al., 2004) from the fMRI passive face and object viewing task used in Chapter Four. Our objectives are two-fold: 1.) *Comprehensively quantify* age differences using measures of extent, magnitude, and lateralization of activation thoughout the entire brain and 2.) *qualify developmental changes* by characterizing neural activation patterns.

As established previously in this work, a fundamental interest of developmental cognitive neuroscience is the changing functional organization of the cortex in relationship to cognitive tasks. Though many neuroimaging studies have limited their investigations to particular cortical regions (i.e. FFA for face processing), cognitive processing is a result of activity within large-scale, distributed interconnected populations of neurons. In Chapter Four, we investigated the maturation of functional neural correlates of face and object processing within the ventral processing stream (VPS). We attributed our finding of developmental shifts in the VPS face-preferential loci to the potential maturation of inter-cortical visual pathways such as later developing frontal lobe connections. In Chapter Five, from our developmental investigation of a structural similarity basis for object processing, we demonstrated that normal visual processing involved frontal, parietal, and cerebellar loci as well as VPS loci. From these experiments and others, data indicate that normal visual processing recruits a network of cortical regions (Andrews & Schluppech, 2004; Chao, Martin, & Haxby, 1999; Epstein & Kanwisher, 1998; Gathers & Joseph, 2003a; George, Evans, Fiori, Davidoff, & Renault, 1996; Haxby et al., 1994; Itier & Taylor, 2004c; Joseph & Farley, 2004; Joseph & Gathers, 2003; Sergent & Bindra, 1981). Thus, a whole-brain approach is warranted in our developmental fMRI study of face and object recognition.

In our whole-brain approach, we employ comprehensive measures to quantify maturational changes. In general, developmental fMRI studies including working memory and face processing investigations report more distributed widespread neural networks in children than adults (Casey et al., 1997; Gaillard et al., 2000; Passarotti et al., 2003; Thomas et al., 1999). However, the definition of "distributed" and measures of distribution vary among imaging studies. Existing developmental fMRI studies report functional developmental changes in three aspects of activation patterns: extent of activation (Casey et al., 1997; Gaillard et al., 2000; Passarotti et al., 2003), signal magnitude (Brown et al., 2004; Thomas et al., 1999), or hemispheric lateralization (Holland & al., 2001; Moses et al., 2002; Passarotti et al., 2003). Regarding the validity and the constraints of each measure (Casey et al., 1997; Gaillard, Grandin, & Xu, 2001b; Muzik, Chungani, Juhasz, Shen, & Chungani, 2000; Palmer, Brown, Petersen, & Schlaggar, 2004), we incorporate all three measures for a complete assessment of functional maturation. Figure 6.1. Furthermore, we consider each measure of functional change at two spatial levels – global and local.

We define global measurements as widespread changes throughout the cortex whereas local measurements refer to regional changes. As mentioned above, the definition of “distributed” activation in developmental literature is unclear. Reports that children recruit more distributed networks for a task than adults may be interpreted in two ways (See Figure 6.1a). Children may recruit a larger *set* of spatially scattered regions of activity across the cortex (a greater number of activated clusters) than adults or children may recruit larger regions of activation than adults (a greater number of voxels per cluster). Global and local assessments of extent allow us to make a distinction in developmental changes in distribution patterns between spatially dispersed and locally diffuse.

Like extent, changes in signal magnitude are also important measures of developmental change (Figure 6.1b). However, when comparing signal strength among age groups, care must be taken to assure signal differences reflect development related to the task rather than physiological or anatomical artifacts of maturation. For instance, Gaillard et al. (Gaillard et al., 2000) noted that maturational differences in respiration rates, head sizes, and skull thickness may enhance or depress signal magnitude readings for one age group over. This concern served as the motivation for our global signal magnitude analysis. To ensure that our signal magnitude findings reflected true developmental changes in response to the task rather than general systematic age-related changes, we statistically compared the overall average percent signal change (collapsing across all regions of activation) among groups. In addition to global signal changes, we analyzed local or regional activation to determine if the roles of regions remain stable or change with development. Anatomical and cellular studies indicate that regions develop at different rates (Giedd et al., 1999; Sowell, Thompson, Tessner, & Toga, 2001; Wilke, Schmithorst, & Holland, 2002). On a functional level, a recent developmental study of reading reports regional increases and decreases in fMRI signals with maturation (Brown et al., 2004). Thus, in regards to evaluating developmental changes in signal magnitude, global and local assessments are needed.

In addition to activation extent and signal magnitude, previous functional neuroimaging studies of maturation have also described development by changes in lateralization (Holland & al., 2001; Mabbott & Smith, 2003; Martinez et al., 1997; Moses et al., 2002; Sowell et al., 2004).

These studies characterized hemispheric changes based on extent and signal strength. Therefore, for hemispheric changes, we assessed global and local levels of extent (Figure 6.1c) and signal magnitude.

Second, we used the conservative hypothesis testing approach, logical combination analysis (Joseph et al., 2002), to qualify functional developmental changes in face and object processing. A primary goal of developmental fMRI studies is to determine changes in neural systems. Another essential goal of developmental neuroimaging is to describe the cognitive processing performed in changing systems (Palmer et al., 2004; Poldrack, 2000). Behavioral evidence suggests that face processing and corresponding brain regions become more specialized with age. Developmental ERP studies have shown that certain electrophysiological components become more sensitive to faces with age (Carver et al., 2003; de Haan et al., 2002; Halit, de Haan, & Johnson, 2003). Similarly, in Chapter Four, we reported finding increased category-selectivity in non-VPS regions with increased age. Thus, to identify potential changes in face (and object) processing linked to developmental changes in neural substrates; we define four main profiles of activation, face-preferential, face-selective, face-manufactured-natural graded, and face-manufactured-natural conjoined (See Appendix A) and applied them to our examination of extent, magnitude, and lateralization of activation.

Based on findings from previous studies, we predict that face and object processing networks in children and adults include regions within and without the ventral processing stream (Gathers, Bhatt, Corbly et al., 2004; Gathers, Piper, Partin, & Joseph, 2001) that narrow anatomically with development (Gauthier & Nelson, 2001). By a functional anatomical narrowing of network activity, we suggest that children initially use a larger set of regions for face and object processing than adults. Furthermore, from previous studies, we predict that within the VPS functional narrowing does not occur; however, in other non-VPS regions, children are less selective in their responses to stimuli than regions recruited by adults (Brown et al., 2004; Carey & Diamond, 1994; Casey et al., 1997; Gathers, Bhatt, Corbly et al., 2004; Holland & al., 2001; Passarotti et al., 2003; Schwarzer, 2000; Thomas et al., 1999). In this chapter, we use two methods of analyses to examine our predictions. One, we quantify fMRI changes in extent, magnitude, and lateralization of activation globally (whole-brain) and locally (regions of interest) to assess distribution changes with age. Two, to assess changes in selectivity to stimuli, we provide a qualitative description of quantitative developmental changes in the face and object recognition networks.

Participants

Child Subjects

Twenty-nine 5-11 year old normal, healthy children volunteers (18 males, 11 females, mean age 8.3 years) with no significant medical histories or conditions were compensated for their participation. All volunteers had normal visual acuity, were fluent in English, and showed a preference for their right hand based on the Edinburgh Handedness Survey. Receptive and expressive language skills were within normal age limits as determined by the Peabody Picture Vocabulary Test (PPVT) (Dunn & Dunn, 1997) and the Expressive Vocabulary Test (EVT) (Williams, 1997). Three children did not complete the study. Data from six other participants were omitted due to excessive head motion. Thus, data from the remaining 20 subjects (12 males, 8 females, mean 8.8 years) were divided into two age groupings, 5-8 year olds and 9-11 year olds, and submitted to further analyses.

Adult Subjects

Nine adult subjects (5 males, 4 females, mean 20.8 years, 8 right-handed) with normal or corrected-to-normal vision and no significant medical or psychological conditions participated in a previously published study (Joseph & Gathers, 2002).

Results

Analysis of Activation Extent

We examined two measures of activation extent, global (whole-brain) and local (regional). Global measures allowed us to investigate claims that neural networks in children consist of more regions of scattered brain activity than in adults. For each subject in each age group, we calculated the global extent of activation expressed as percentage of total clusters in a whole-brain volume for each activation profile (face-, manufactured-, or natural-selective, fix-selective, face-preferential, face-graded, and conjoined). Using local measures of extent, we investigated developmental growth or regression as regional changes in dispersion. Specifically, we defined the local extent of activation as the average size of each cluster for each activation profile. The number of clusters for category-selective (M, N, F) activation was very low and not all participants had category-selective responses. In fact, out of a total of 1846 clusters detected in individual subjects, only four clusters were detected for face-selective activation, 18 for natural-selective activation, and four for manufactured-selective activation. Due to the paucity of category-selective data in individual subjects, we did not analyze extent of category-selectivity. Instead, we determined the extent of conjoined, face-preferential, and face-graded activity. When comparing age groups in developmental fMRI studies, similarities and differences in the control task activation for each population must be considered for proper interpretation of task activations (Palmer et al., 2004). Therefore, in addition to our experimental conditions (F, M, N), we examined the extent of fixation-selective (baseline) activation to assess the validity of our control task among age groups. We submitted the two measures of activation extent (number and size of clusters) to separate random-effects, two-way ANOVAs with age group (adults, ages 9-11 years, and ages 5-8 years) as a between-subjects factor and profile (face-graded, face-preferential, conjoined, and fixation-selective) as a within-subjects factor.

Global Analysis of Activation Extent

As shown in Figure 6.2a, fixation-selective (baseline) and conjoined clusters were more numerous than face-graded or face-preferential clusters, as confirmed by the main effect of profile [$F(3,24)=31.2$, $p<.0001$]. The overall age effect, however, was not significant [$F(2,26) =1$, $p<.43$], indicating that adults and children activate the same number of clusters when all brain regions and profiles are considered collectively. Nevertheless, the significant age x profile interaction [$F(6,48) = 4.2$, $p< .002$] indicated that the number of clusters for a given profile type depended on age. To further explore this interaction, we conducted simple main effects analyses of age for each profile separately. The only significant effect of age emerged for the conjoined profile [$F(2,26)= 5.7$, $p< .009$] in which 5-8 year olds activated more clusters than did adults ($p< .007$, Bonferroni corrected) but not more than children ages 9-11 years ($p< .20$). Thus, children activate a greater number of conjoined clusters than adults.

Local Analysis of Activation Extent

With respect to our local measure of activation extent, cluster size, Figure 6.2b illustrates that adults activated much larger conjoined clusters than any other profile or age group. Hence, the main effect of profile was significant [$F(3,24) = 27.9$, $p < .0001$], as was the age effect [$F(2,26) = 10.6$, $p < .0001$] and the age x profile interaction [$F(6,48) = 3.9$, $p < .003$]. Simple main effects analyses of age conducted separately for each profile type revealed that the age effect was only significant for the conjoined profile ($\underline{p} < .0001$) and not the other three profiles ($\underline{p} < .17$). In sum, the analyses of activation extent revealed that adults activated fewer but larger conjoined clusters than children, but fixation-selective, face-graded, and face-preferential activation showed no differences in extent as a function of age.

Global Analysis of Signal Magnitude

In addition to extent, we performed global and local assessments of magnitude as measured by percentage signal change for each category (F, M, N). We conducted a global effects analysis, across all activation profiles and brain regions, to determine if signal strength was a phenomenon of age (Gaillard et al., 2000). To assess potential differences in general signal strength throughout the developing brain, we submitted the average percent signal change of each category for each subject across regions and profiles to a repeated-measures ANOVA with category (F, M, N) as the within-subject factor and age (adults, 9-11 years, 5-8 years) as the between-subjects factor. The within-subject factor of category along with the between-subjects factor of age allowed us to discern if differences in overall magnitude could be attributed to stimulus category or to age. As depicted in Figure 6.3, results of the global analysis revealed no significant effect of age [$F(2,26) = .720$, $\underline{p} < .496$] for signal magnitude implying no systematic change in signal intensity with age. Thus, no systematic signal intensity changes occurred with age.

Local Analysis of Signal Magnitude

In addition to global magnitude, we assessed local magnitude to discern if significant signal differences occurred regionally as a result of maturation. We submitted each region of activation confirmed by ROI analyses to repeated-measures ANOVAs where category (F, M, N) served as the within-subject factor and age (adults, 9-11 years, 5-8 years) as the between-subjects factor. The main effect of age was significant for 28 regions of activation (See Tables 6.1a, 6.2a, and 6.3a) including clusters of conjoined, face-preferential, face-graded, and fixation-selective activation profiles. In seven of these regions, the main effect of category was significant and in six regions a significant interaction occurred between category and age. All regions significant for the main effect of category or the interaction of category x age were explained by face-graded or face-preferential profiles.

We characterized maturational trends in regional magnitude changes as either progressive (signal increases) or regressive (signal decreases). We submitted the 28 regions with a significant main effect of age to a simple linear regression. See Tables 6.1b, 6.2b, and 6.3b. Collapsing across category, age predicted average percentage signal change in 11 of the 28 regions. These regions were significant for either linear increases (progression) or decreases (regression) in signal with age. In addition, as evidenced by p-values, trends of increasing or decreasing activation with age occurred in 17 other clusters; however, these were neither significant nor linear but instead were characterized by non-linear U-shaped and inverted U-shaped functions where children 9 to 11 years of age had either significantly greater or lesser signal strength than children 5 to 8 years and adults. Here, we focused only on regions with linear changes in magnitude. In general, linear increases in signal magnitude (progressive changes) occurred in occipito-temporal cortex, bilateral fusiform gyrus and right cuneus, and superior and inferior parietal regions whereas linear decreases in signal magnitude (regressive changes) were found in frontal (superior, middle, and inferior) and superior temporal regions. The only "selective" clusters with a significant age effect were fixation-selective clusters. No category-selective clusters survived the analyses. Of thirty-eight significant fixation-selective ROI's, only three were significant for linear changes in signal as a function of age. Five fixation-selective clusters showed non-linear trends of signal change. Thus, in evaluating the control condition across age groups, developmental differences appeared in only eight of the 38 baseline regions. Overall, local analyses revealed both progressive and regressive regional age effects of magnitude for clusters with conjoined, face-graded, face-preferential, and fixation-selective activation profiles. (See Figures 6.4 and 6.5 and Tables 6.1b, 6.2b, and 6.3b)

Lateralization Analysis of Extent

To assess lateralization differences in extent among age groups, we computed the average number of clusters (global analysis) and the average cluster size (local analysis) within each hemisphere for each subject. We submitted these data to separate three-way mixed ANOVAs with age as a between-subjects factor and hemisphere (right, left) and profile (face-graded, face-preferential, fixation-selective, and conjoined) as within-subject` factors. If maturation results in more lateralization, as reported in other studies (Holland & al., 2001; Moses et al., 2002), then we expected a significant hemisphere x age interaction, which may or may not be qualified by profile type. For number of clusters, neither the hemisphere x age interaction nor the hemisphere x age x profile interactions were significant.

However, for cluster size, the hemisphere x age interaction was significant [F(2, 26) = 4.5, $p < .002$]. As shown in Figure 6.6, adults have significantly larger clusters of activation in the right hemisphere than in the left, whereas both groups of children have equally large clusters in the two hemispheres. This interaction was not further qualified by profile type (i.e. the hemisphere x age x profile interaction was not significant, $p < .17$), suggesting that greater right hemisphere interaction in adults persists across all profile types.

Lateralization Analysis of Magnitude

In addition to evaluating potential changes in lateralization extent among age groups, we considered hemispheric changes in signal magnitude. Using a mixed 3-way ANOVA with category (F, M, N) and hemisphere (right or left) as within subject variables and age group as the between subject variable, data indicated a significant age x hemisphere interaction [F(2, 26) = 6.328, $p < .006$]. Main effects of age [F(2, 26) = .657, $p < .527$] and hemisphere [F (1, 26) = .011, $p < .916$] were not significant. Thus, overall magnitude changes did not exist but were a factor of age. As age increased, signal magnitude increased in the right hemisphere but decreased in the left hemisphere. This coincides with extent findings. With age, activation within the right hemisphere grows in cluster size and signal strength. Signal magnitude was significant for category but no interactions with category were significant. Therefore, lateralization analyses were collapsed across categories.

Discussion

With these analyses, we contributed to the limited data regarding the normal functional maturation of face and object processing networks. We quantified and qualified developmental changes in activation patterns using global (whole-brain) and local (regional) analyses of extent, magnitude, and lateralization of activation. We proposed that face and object processing involve neural networks that extend beyond the VPS and undergo anatomical narrowing with maturation. Based on data indicating maturational changes in neuroanatomical (Benes, Turtle, Khan, & Farol, 1994; Fuster, 2002; Gaillard et al., 2001a; Giedd et al., 1999; Sowell, Thompson, Holmes, Batth et al., 1999; Sowell, Thompson, Holmes, Jernigan, & Toga, 1999; Sowell et al., 2001; Wilke et al., 2002) and cognitive processes (Carey & Diamond, 1994; Schwarzer, 2000), we predicted a developmental redistribution of functional activation patterns from widespread recruitment of cortical regions in young children, including frontal and parietal activation, to more focal VPS activation in adults (Brown et al., 2004; Carey & Diamond, 1994; Casey et al., 1997; Gathers, Bhatt, Corbly et al., 2004; Holland & al., 2001; Passarotti et al., 2003; Schwarzer, 2000; Thomas et al., 1999).

Extent

In analyzing the maturation of face and object processing networks, we considered global (number of clusters) and local (cluster size) measures of extent. Changes in extent were not all systematic and did not include all activation profiles. Global assessment of extent (number of clusters) revealed no systematic changes. As a control for extent, we examined fixation-selective activity (baseline). Adults and children aged 5 to 8 years yielded significantly more fixation-selective clusters than subjects 9 to 11 years eliminating the issues of general processing changes or overall extent effects with increasing age.

In addition to findings in fixation-selective activation extent, global analysis revealed a significant developmental difference in conjoined activation. Both child groups had significantly more conjoined clusters than adults with children nine to eleven years of age having significantly more conjoined clusters than children five to eight years. Our findings are supported by other developmental fMRI studies. For example, in a study of verbal fluency, Gaillard et al. also found that children activate significantly more pixels than adults (2000). These developmental differences in cluster numbers may reflect underlying structural modifications. Changeux and Danchin proposed a neuronal plasticity theory in which excess of labile synaptic connections exist during development (1976). Over time, some connections are incorporated into functioning systems and become stable while other redundant connections fail to be incorporated and are eliminated. More recent findings of decreases in synaptic density support this idea. Huttenlocher (1990) reported a developmental decrease in synaptogenesis with regional differences in rates of loss. Age-related elimination of synapses may explain a reduction in the number of activated clusters from childhood to adulthood.

We also found significant local developmental changes in extent of activation. For conjoined activation profiles (non-category specific) only, located primarily in the occipito-temporal cortex, adults produced significantly larger clusters of activity than children. As with global results, these age-related regional increases may reflect structural changes. In fact, animal studies have shown that increased cortical thickening and arborization occur as a result of enriched environmental experience (Diamond, 2001). Because clusters that "grew" in extent were located in cortex known to process visual stimuli, it follows that these areas show age-related increases based on usage or experience with visual tasks. Thus, age-related functional changes in local activation extent (cluster size) may signify experience-based structural changes.

Taken together, our global and local extent results indicated that adults have a significantly smaller number of conjoined clusters than either child group but that these clusters are significantly larger than those in children. Synaptic reduction with age would explain developmental decreases in cluster number whereas increased cortical thickening and arborization with experience would explain developmental increases in cluster size. Thus, our fMRI findings of developmental changes in extent, both globally and locally, may link functional developmental changes to changes in brain structure.

Magnitude

As with extent of activation, we evaluated global and local changes in signal magnitude with age. We detected no significant global changes in magnitude as a function of age. In fact, stimulus category (F, M, N) not age was found to be significant for overall magnitude changes. Thus, we determined that magnitude could be used as a basis of comparison in developmental fMRI studies without fear of age-related biological factors systematically influencing general signal strength (Gaillard et al., 2000).

In local magnitude analysis, twenty-eight brain regions displayed a significant effect of age on percent signal change. Eleven of the twenty-eight regions were characterized by linear increases (progression) or decreases (regression) in signal strength with age. Linear magnitude findings existed as positive and negative increases (progression) and decreases (regression) relative to baseline (See Figures 6.4 and 6.5). Positive increases relative to baseline occurred in the occipito-temporal cortex while negative increases were focused in parietal cortex. In contrast, linear decreases occurred in frontal regions (positive), the superior temporal lobule (negative), and the paracentral lobule (negative). These developmental activation patterns in signal magnitude are supported by both structural and cognitive literature. Our findings of regional changes in magnitude with age, like our results for extent, correspond with maturation studies regarding brain structure (Giedd et al., 1999; Sowell et al., 2001; Wilke & Holland, 2003). Our regional magnitude and extent findings may be founded on similar explanations of structural development. As noted in our discussion of extent, Huttenlocher (1990) found regional differences in developmental rates of synaptic loss. He noted slower declines in the synaptic density of occipital regions than frontal regions. Furthermore, Sowell et al. found age effects for gray matter density reduction in frontal and parietal cortex from childhood to adolescence and frontal gray matter density reductions from adolescence to adulthood (Sowell, Thompson, Holmes, Batth et al., 1999; Sowell et al., 2001). Thus, linear magnitude decreases in frontal regions and increases in occipital regions correspond to cellular maturation processes such as synaptic pruning (Huttenlocher, 1990), gray matter modification (Sowell, Thompson, Holmes, Jernigan et al., 1999; Sowell et al., 2001) and refinement of white matter fiber tracts (Schmithorst, Wilke, Dardzinski, & Holland, 2002; Sowell et al., 2004).

Our regional magnitude measures for face and object processing are also in alignment with developmental fMRI studies of other cognitive processes. In their study of inhibition, Bunge and colleagues noted that, in general, children and adults had different abilities for recruiting different brain regions and, in a developmental study of reading (Bunge, Dudukovic, Thomason, Vaidya, & Gabrieli, 2002), Brown et al. found regions of progressive and regressive signal changes as a function of age (2004). Furthermore, in their developmental study of reading, Brown and colleagues found that regional age-related increases in signal corresponded to regions traditionally recognized as primary players in language and reading tasks. Similar to Brown et al., we found developmental increases in magnitude, as well as extent, in regions attributed to visual processing – occipito-temporal regions. Thus, structural changes driven by experience or task may explain age-related linear increases in signal magnitude as well as age-related changes in cluster size. Hence, magnitude findings may be task-relevant in nature.

Lateralization

Based on other developmental fMRI studies that cite lateralization with age (Holland & al., 2001; Moses et al., 2002; Sowell et al., 2004), we examined maturation in regards to changes in hemispheric extent and magnitude. As with our other measures of change, we assessed lateralization at both global and local levels. Lateralization analyses revealed increasing cluster size (local extent) and signal strength in the right hemisphere with age regardless of profile type. These age-related functional hemispheric changes are expected as they correspond with findings of structural and cognitive maturation. Using EEG to measure strength and the number of neuronal connections, Thatcher, Walker and Giudice noted differential development of the hemispheres with a lag in the right hemisphere (1987). Using diffusion tensor imaging, Klingberg et al. reported a significant difference in axonal organization in the right hemisphere versus the left but no significant differences in myelination (Klingberg, Vaidya, Gabrieli, Moseley, & Hedehus, 1999). Similar to these anatomical studies, we find age-related functional changes particular to the right hemisphere.

Functional hemispheric changes may reflect structural changes influenced by cognitive development. Previous developmental studies imply that lateralization may occur as a result of changes in cognitive processing (i.e. global vs local; face processing) or task-related competency (i.e. left lateralized for language). In fact, in a study of global and local processing of facial features Moses et al. (2002) noted greater right occipito-temporal activation than left for global processing with maturity and, in a verb generation task , Holland et al. (2001) found increased left hemisphere activity with age. In addition, others have implied specific categorical processing result in lateralization (i.e. face recognition lateralized to the right hemisphere) (Kanwisher et al., 1997). Because current analyses reveal hemispheric changes with development across all categories regardless of activation profile, this study does not support category-specific lateralization. Our findings indicate developmental changes in lateralization are more likely driven by cognitive processing or task rather than stimulus category.

Table 6.1a Signal Magnitude ANOVA Results: Local Linear Developmental Changes

region	BA	Taliarach (x,y,z)	Cluster size (voxels)	Repeated Measures ANOVA of percent signal change/ category		
				Effect of Age	Effect of Category	Age x Category
R. Cuneus	18	21, -99, 7	65	F(2,26) = 3.2**	F(2,52) = .20	F(4,52) = .30
R. FG	37	38, -58, -20	494	F(2,26) = 6.9**	F(2,52) = 2.8	F(4,52) = .40
L. FG	18	-34, -75, -14	2399	F(2,26) = 7.7**	F(2,52) = 3.0	F(4,52) = .90
L. SPL	7	-31, -60, 54	81	F(2,26) = 11.1**	F(2,52) = 1.7	F(4.52) = 1.2
L. IPL	40	-63, -27, 35	99	F(2,26) = 3.8 **	F(2,52) = 2.1	F(4,52) = .80
R. Paracentral	7	3, -42, 49	1171	F(2,26) = 9.9 **	F(2,52) = 2.1	F(4,52) = 1.3
R. MFG	10	52, 45, -12	148	F(2,26) = 32.2**	F(2,52) = 1.5	F(4,52) = .40
L. SFG	6	-4, 10, 68	11	F(2,26) = 7.9**	F(2,52) = 8.4 **	F(4,52) = 3.7**
L. IFG	47	-49, 27, -21	31	F(2,26) = 8.2**	F(2,52) = 1.0	F(4,52) = .40
L. STG	21	-51, -13, -2	77	F(2,26) = 4.7**	F(2,52) = .20	F(4,52) = .40

Note. R, right; L, left; FG, fusiform gyrus; SPL, superior parietal lobule; IPL, inferior parietal lobule; MFG, middle frontal gyrus; SFG, superior frontal gyrus; IFG, inferior frontal gyrus; STG, superior temporal gyrus; BA, Brodmann's area; x, medial-lateral coordinate; y, anterior-posterior coordinate; z, inferior-superior coordinate; SS, structural similarity. ** indicates significance of $p < .05$.

Table 6.1b Signal Magnitude Regression Results: Local Linear Developmental Changes

region	BA	Regression (F/p values)	Signal Trend	Activation Profile
R. Cuneus	18	F(1,27) = 4.1, p < .054	Increase	Face-Object-Graded
R. FG	37	F(1,27) = 15.1, p < .001	Increase	Conjoined
L. FG	18	F(1,27) = 16.8, p < .000	Increase	Conjoined
L. SPL	7	F(1,27) = 18.2, p < .000	Increase	Conjoined
L. IPL	40	F(1,27) = 2.0, p < .168	Increase	Fixation-Selective
R. Paracentral	7	F(1,27) = 21.1, p < .000	Decrease	Fixation-Selective
R. MFG	10	F(1,27) = 10.7, p < .003	Decrease	Conjoined
L. SFG	6	F(1,27) = 6.5, p < .017	Decrease	Face-Object-Graded
L. IFG	47	F(1,27) = 9.6, p < .005	Decrease	Conjoined
L. STG	21	F(1,27) = 10.7, p < .003	Decrease	Fixation-Selective

Note. R, right; L, left; FG, fusiform gyrus; SPL, superior parietal lobule; IPL, inferior parietal lobule; MFG, middle frontal gyrus; SFG, superior frontal gyrus; IFG, inferior frontal gyrus; STG, superior temporal gyrus; BA, Brodmann's area; x, medial-lateral coordinate; y, anterior-posterior coordinate; z, inferior-superior coordinate; SS, structural similarity.

Table 6.2a Signal Magnitude ANOVA Results: Local Non-Linear U-Shaped Developmental Changes

region	BA	Taliarach (x,y,z)	Cluster size (voxels)	Repeated Measures ANOVA of percent signal change/ category		
				Effect of Age	Effect of Category	Age x Category
R. MTG	21	44, -56, 6	21	F(2,26) = 5.1**	F(2,52) = 8.3**	F(4,52) = 4.1**
R. FG	37	42, -56,-22	19	F(2,26) = 4.6**	F(2,52) = .60	F(4,52) = 1.7
L. OG	17	28, -96, -14	60	F(2,26) = 4.0**	F(2,52) = .10	F(4,52) = 2.1
L. FG	18	-32, -85, -19	64	F(2,26) = 5.2**	F(2,52) = 8.1**	F(4,52) = 4.0**
L. Postcentral	1	-57, -15, 54	256	F(2,26) = 7.7**	F(2,52) = 3.0	F(4,52) = .90
L. Cuneus						
R. Postcentral	1	48, -26, 64	42	F(2,26) = 3.7 **	F(2,52) = .60	F(4,52) = .20
R. OG	17	26, -97,-13	32	F(2,26) = 4.7**	F(2,52) = 7.8**	F(4,52) = 3.4**
L. IPL	7	-40, -60, -56	34	F(2,26) = 4.8**	F(2,52) = 2.0	F(4,52) = 3.4**
L. FG	18	-32, -85, -19	65	F(2,26) = 5.1**	F(2,52) = 8.3**	F(4,52) = 4.1**

Note. R, right; L, left; MTG, middle temporal gyrus; FG, fusiform gyrus; OG, occipital gyrus; IPL, inferior parietal lobule; BA, Brodmann’s area; x, medial-lateral coordinate; y, anterior-posterior coordinate; z, inferior-superior coordinate; SS, structural similarity. ** indicates significance of $p < .05$.

Table 6.2b Signal Magnitude Regression Results: Local Non-Linear U-Shaped Developmental Changes

region	BA	Regression (F/p Values)	Signal Trend	Activation Profile
R. MTG	21	F(1,27) = .80, p < .367	Increase	Face-Object-Graded
R. FG	37	F(1,27) = 8.7, p < .007	Increase	Face-Object-Graded
L. OG	17	F(1,27) = .00, p < .948	Increase	Face-Preferential
L. FG	18	F(1,27) = 1.5, p < .233	Increase	Face-Object-Graded
L. Postcentral	1	F(1,27) = 2.3, p < .144	Increase	Conjoined
L. Cuneus	17	F(1,27) = .90, p < .361	Increase	Face-Preferential
R. Postcentral	1	F(1,27) = 1.2, p < .296	Decrease	Conjoined
R. OG	17	F(1,27) = .00, p < .969	Decrease	Face-Object-Graded
L. IPL	7	F(1,27) = .10, p < .755	Decrease	Conjoined
L. FG	18	F(1,27) = .40, p < .515	Decrease	Face-Preferential

Note. R, right; L, left; MTG, middle temporal gyrus; FG, fusiform gyrus; OG, occipital gyrus; IPL, inferior parietal lobule; BA, Brodmann's area; x, medial-lateral coordinate; y, anterior-posterior coordinate; z, inferior-superior coordinate; SS, structural similarity.

Table 6.3a Signal Magnitude ANOVA Results: Local Non-Linear Inverted U-Shaped Developmental Changes

region	BA	Taliarach (x,y,z)	Cluster size (voxels)	Repeated Measures ANOVA of percent signal change/ category Effect of Age	 Effect of Category	 Age x Category
R. Insula	13	47, -14, 12	306	F(2,26) = 11.3**	F(2,52) = .50	F(4,52) = 3.5
R. Precentral	4	28, -28, 58	445	F(2,26) = 9.1**	F(2,52) = .40	F(4,52) = 1.6
L. Cingulate	17	28, -96, -14	84	F(2,26) = 6.0**	F(2,52) = .10	F(4,52) = 2.1
R. IFG	45	48, 20, 20	437	F(2,26) = 3.8 **	F(2,52) = .30	F(4,52) = 2.2*
R. Transverse	41	55, -22, 11	219	F(2,26) = 4.5**	F(2,52) = .10	F(4,52) = .60
R. STG	22	52, -7, -1	86	F(2,26) = 7.2**	F(2,52) = .30	F(4,52) = .60
L. STG	20	-38, 0, -36	30	F(2,26) = 7.2**	F(2,52) = 2.2	F(4,52) = 2.0

Note. R, right; L, left; IFG, inferior frontal gyrus; STG, superior temporal gyrus; BA, Brodmann's area; x, medial-lateral coordinate; y, anterior-posterior coordinate; z, inferior-superior coordinate; SS, structural similarity. ** indicates significance of p < .05.
* indicates significance of p < .01.

Table 6.3b Signal Magnitude Regression Results: Local Non-Linear Inverted U-Shaped Developmental Changes

region	BA	Regression (F/p Values)	Signal Trend	Activation Profile
R. Insula	13	F(1,27) = 1.0, p < .319	Increase	Fixation-Selective
R. Precentral	4	F(1,27) = 1.6, p < .211	Increase	Fixation-Selective
L. Cingulate	17	F(1,27) = 2.5, p < .127	Increase	Fixation-Selective
R. IFG	45	F(1,27) = .70, p < .397	Decrease	Conjoined
R. Transverse	41	F(1,27) = 7.9, p < .009	Decrease	Fixation-Selective
R. STG	22	F(1,27) = 9.9, p < .004	Decrease	Fixation-Selective
L. STG	20	F(1,27) = .10, p < .767	Decrease	Conjoined

Note. R, right; L, left; IFG, inferior frontal gyrus; STG, superior temporal gyrus; BA, Brodmann's area; x, medial-lateral coordinate; y, anterior-posterior coordinate; z, inferior-superior coordinate; SS, structural similarity.

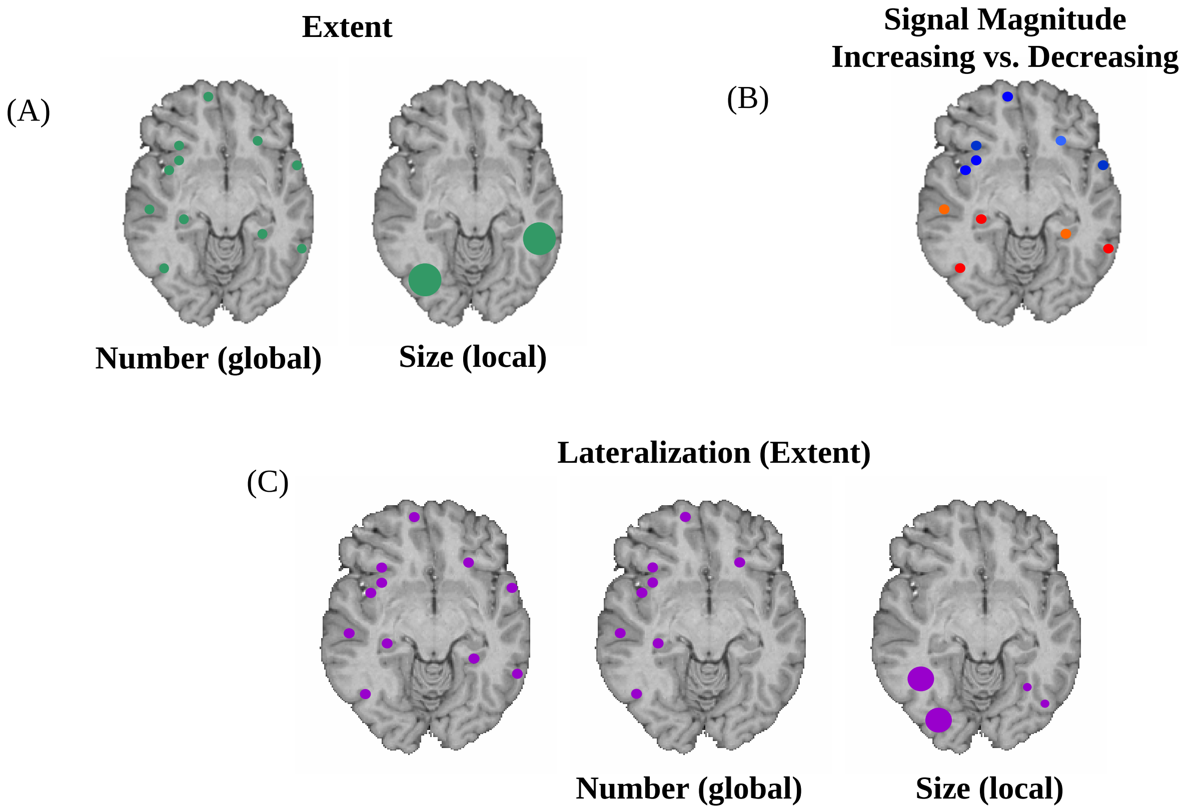


Figure 6.1. Methods of assessing changes in extent, magnitude, and lateralization of activation with age. (A) Extent of activation (i.e. distribution) was assessed at the global level defined by the number of clusters (percentage of clusters) in each group and the local level defined by average cluster size in each age group. (B) Signal magnitude was defined as progressive changes that show increasing signal strength with age (orange, red) or regressive changes that are indicated by a decrease in signal strength (blues). (C) Lateralization of activation was measured at global and local levels of extent and magnitude of activation to assess hemispheric changes in face processing with age.

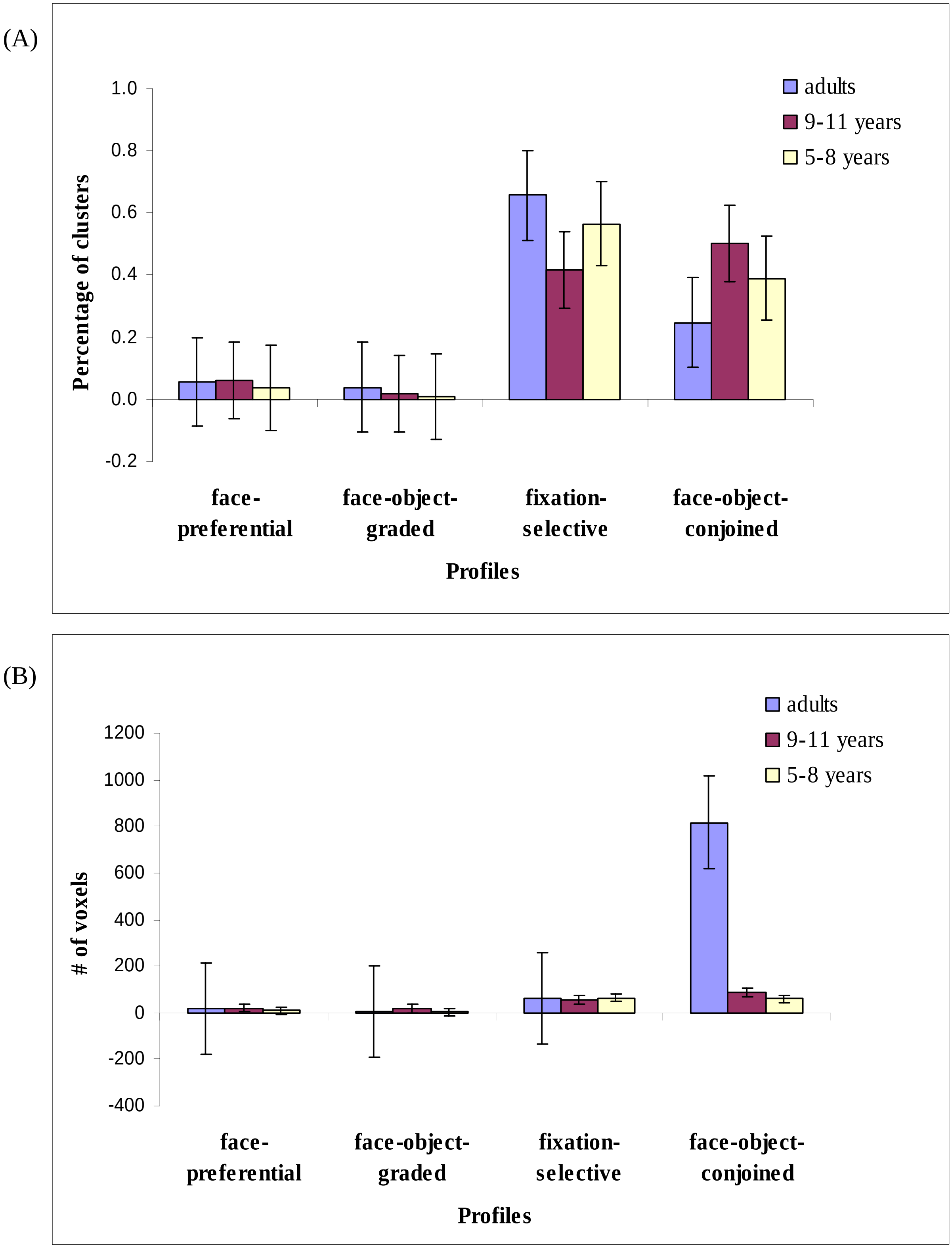


Figure 6.2. Extent of activation via (A) global measures – percentage of clusters and (B) local measures – average cluster size. Error bars reflect standard error of the mean.

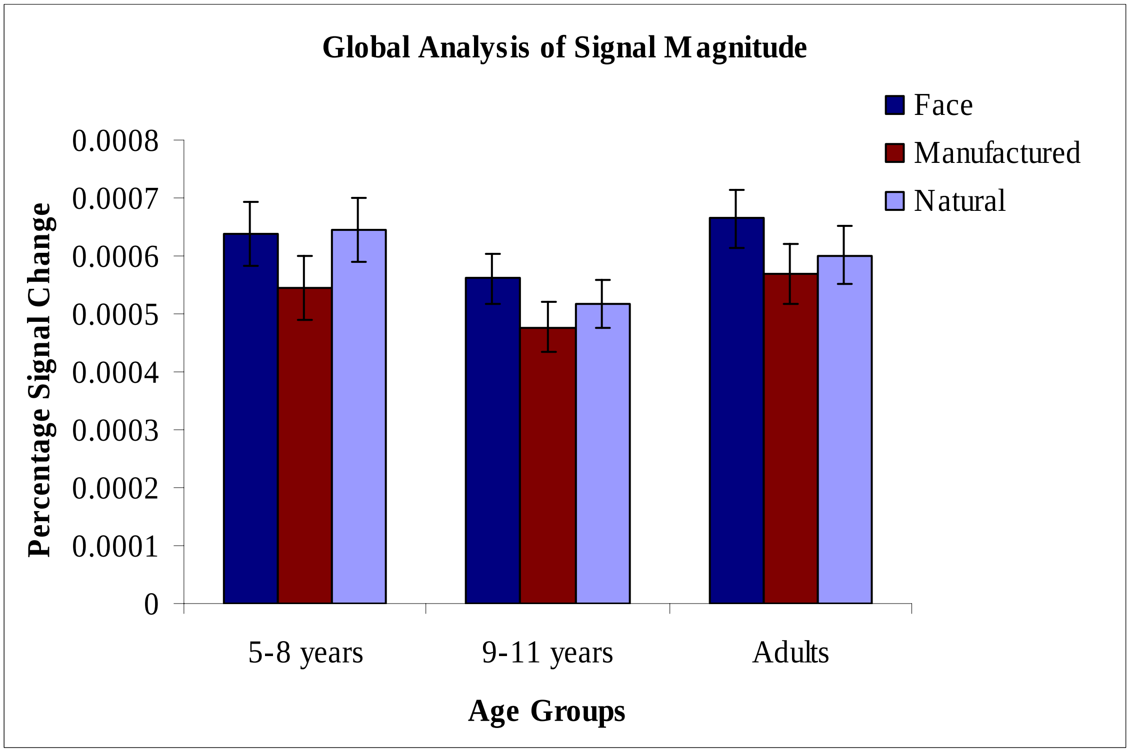
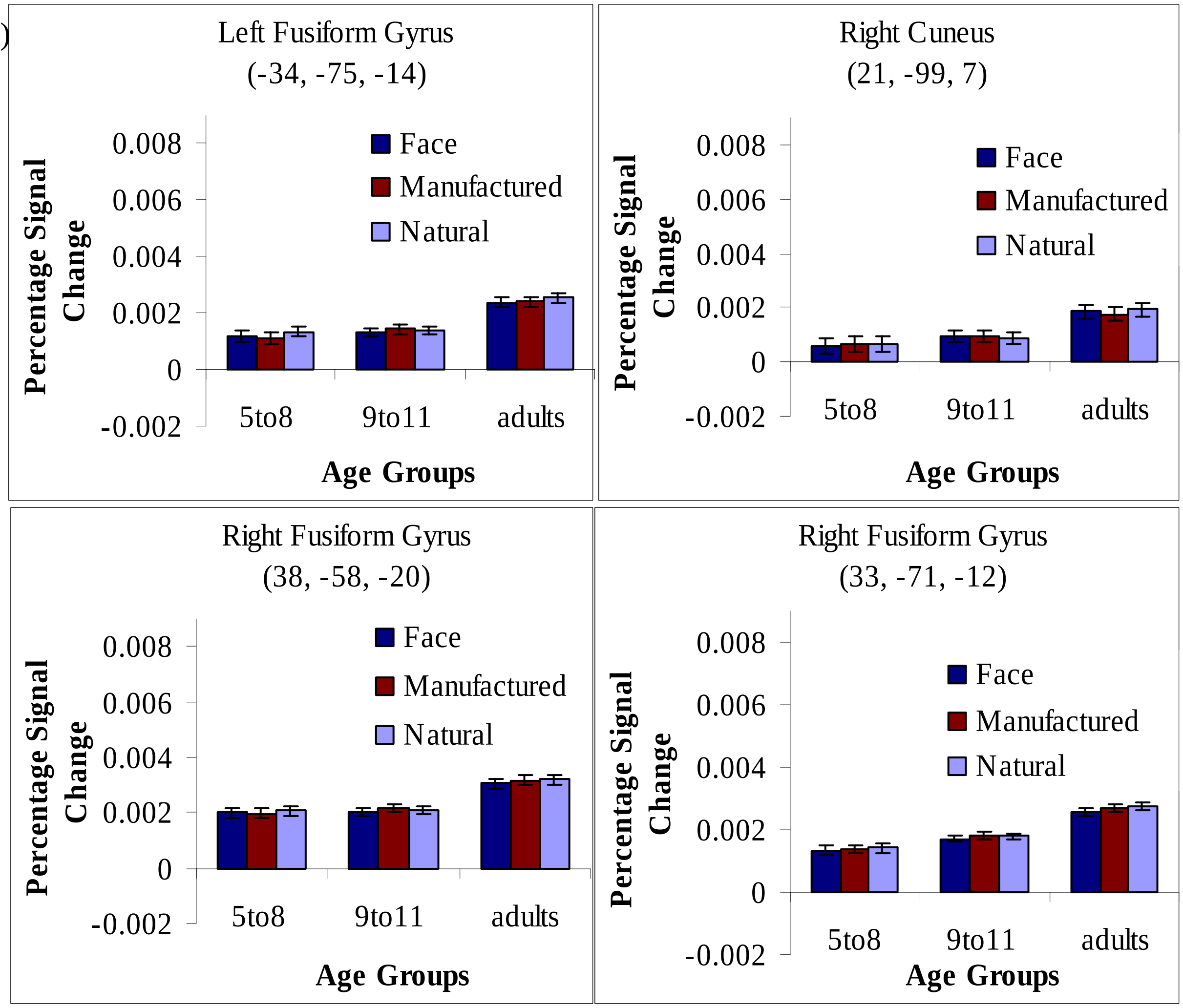


Figure 6.3. Global analysis of signal magnitude results from a repeated measures ANOVA of category (F, M, N) as the within-subject factor and age (5-8 years, 9-11 years, adults) as the between-subjects factor. Error bars reflect confidence intervals based on mean squared error.

(A)



(B)

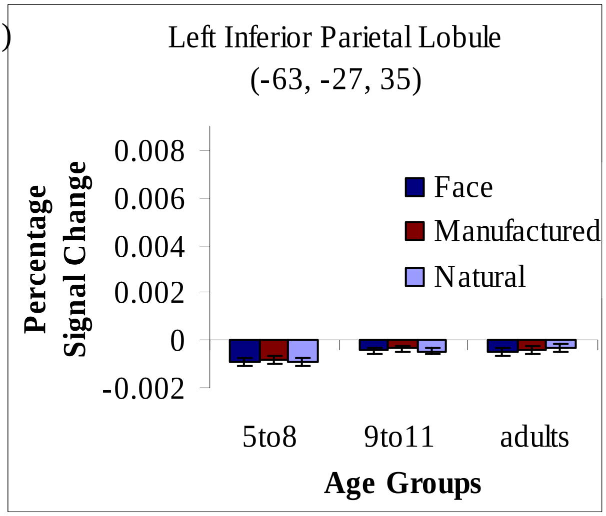


Figure 6.4. Progressive regional changes in signal magnitude. Local magnitude analyses revealed systematic increases in percentage signal change with increasing age in (A) occipito-temporal cortex and (B) parietal regions. Error bars represent within-group confidence intervals.

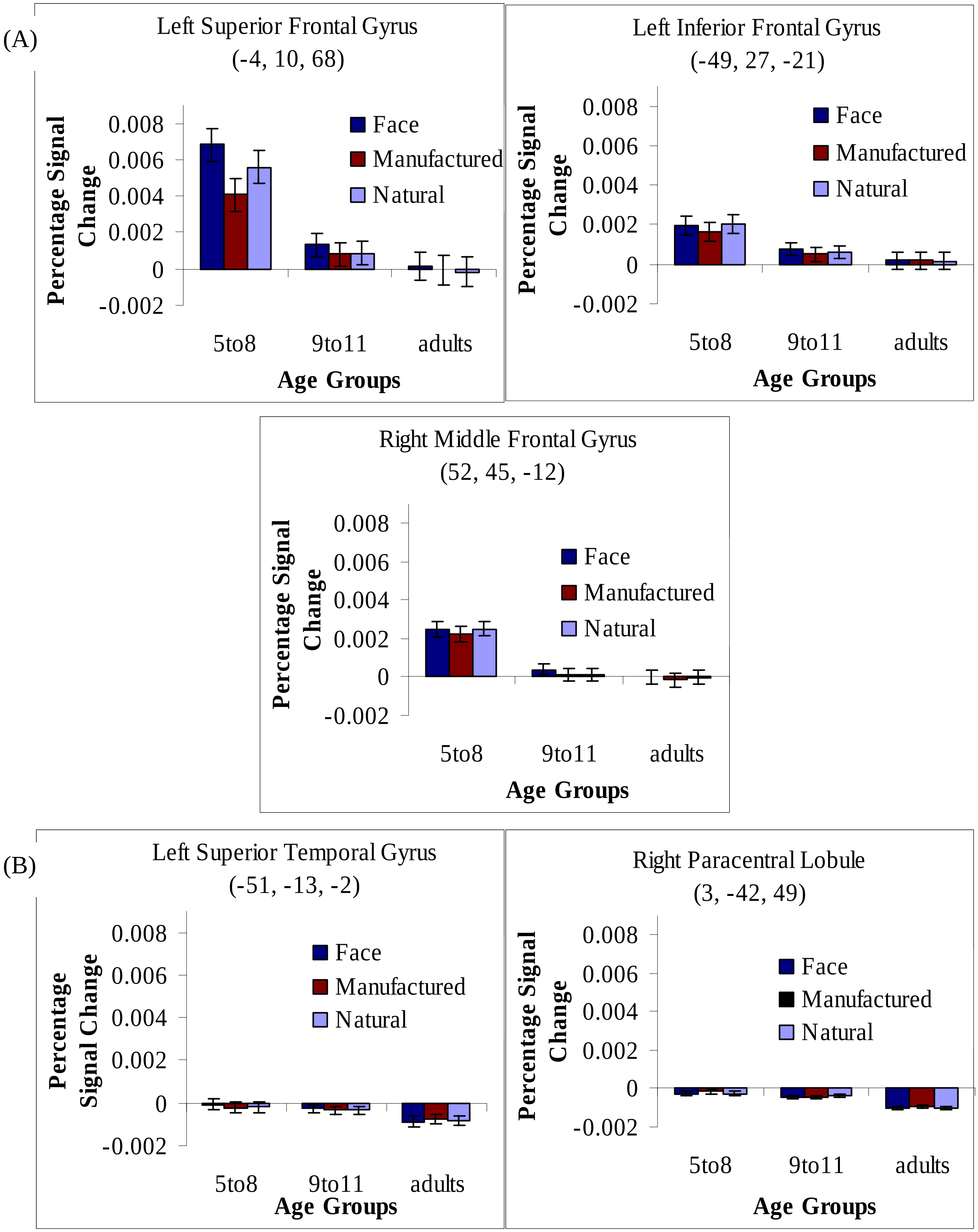


Figure 6.5. Regressive regional changes in signal magnitude. Local magnitude analyses revealed linear decreases in percent signal change with increasing age in (A) frontal and (B) temporal regions. Error bars represent within-group confidence intervals.

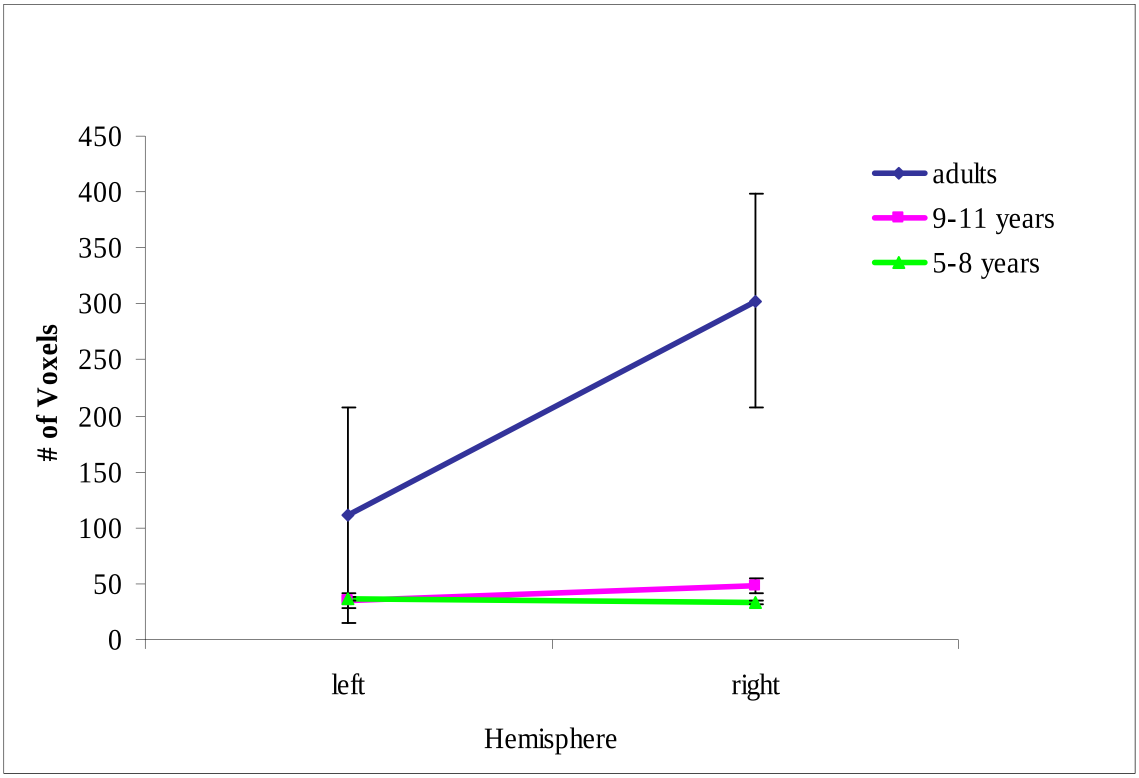


Figure 6.6. Hemispheric distribution by average cluster size (# of voxels) for each age group. Error bars represent standard error of the mean.

Chapter Seven: Conclusions

Motivations and Foundations

"It is the common wonder of all men how among so many (millions of) faces, there should be none alike." Thomas Browne, Religio Medici

Sighted humans are bombarded with countless faces and objects that must be differentiated and identified for proper functioning in society. To the typical adult, differences among faces and objects are distinguishable but, to the individual who suffers from visual processing deficits such as prosopagnosia (an inability to recognize faces) and autism spectrum disorders, the world is a confusing place. Because of their relevance to our daily lives, face and object processing have been investigated for decades. Behavioral methods as well as more recent functional imaging technologies such as ERP, PET, and fMRI, have provided much information on adult visual processing. However, normal developmental processes regarding neural substrates and underlying cognitive mechanisms of face and object recognition remain relatively uncharted.

Though behavioral data indicate developmental changes in face processing from childhood to adulthood (Carey & Diamond, 1994; Schwarzer, 2000), few pediatric neuroimaging studies have investigated functional changes in the neural correlates of face and object processing (Aylward et al., 2005; Carver et al., 2003; de Haan et al., 2002; Halit et al., 2000; Passarotti et al., 2003) with even fewer focusing on changes in early, middle, and late childhood (Want et al., 2003). The establishment of normative data on the maturation of cortical networks of face and object recognition and their underlying cognitive mechanisms is vital in understanding the neurobiology of both normal and abnormal visual processing. Thus, the significance yet shortage of developmental studies of face and object processing served as the motivation for this project.

Gaps in the literature motivated the project and previous adult fMRI studies provided the foundation for our experiments. Findings from three of our adult visual recognition studies indicated a distributed rather than domain-specific modular VPS architecture (Joseph & Gathers, 2002; Joseph et al., 2003). In these fMRI experiments, faces, objects, and letters produced differential rather than selective VPS responses. Thus, our adult data failed to support the idea of a taxonomic based VPS functional organization.

As an alternative, we proposed that a structural similarity (SS) mechanism explained the functional organization of face and object recognition in the VPS. In other words, VPS neural substrates are sensitive to the degree of structural overlap (structural similarity) between stimuli rather than to the categorical distinctions of stimuli. Using a set of same/different matching tasks, we tested the structural basis of VPS organization by parametrically manipulating structural overlap in pairs of animal and shape stimuli (Joseph & Gathers, 2003). Analyses revealed that our manipulations of SS in both animal and shape stimuli modulated fMRI signal in the fusiform gyrus. In particular, more anterior regions of the fusiform gyrus were responsive to high SS processing whereas relatively more posterior regions were sensitive to low SS processing. These findings supported our hypothesis that object structure rather than category determines the functional organization of the VPS. This idea provided the basis for our examination in Chapter Five of the relationship between structural processing and fMRI responses in the child's brain. Collectively, our preliminary adult data served as the starting point for the present set of experiments. In this project, we extended the ideas and the results discussed above to determine the typical neural substrates and cognitive processes of face and object recognition in children five-to-eleven years of age. To outline developmental changes from childhood to adulthood, we compared our child data to adult data.

Findings, Implications, and Future Directions

In Chapter 4, we used a passive face and object-viewing task to identify the VPS neural correlates of face and object processing in children 5-8 years and 9-11 years of age. We compared child findings with data from a similar adult study (Joseph & Gathers, 2003). From the results, two developmental findings emerged. Of primary interest, though all age groups showed face-preferential activation in the ventral processing stream, the location of this activation shifted with age. Adults and children 9-11 years exhibited face-preferential loci near the classically defined fusiform face area, whereas children 5-8 years showed this activation in the posterior ventral processing stream. In addition, the degree of category-selectivity in other brain regions increased with age. While there were no category-selective regions in 5-8 years olds, 9-11 year olds and adults had selective activation for all three stimulus categories (faces, natural objects, and manufactured objects) in non-VPS regions. Although the total number of category-selective voxels increased with age, there were few selective clusters overall and those that emerged were small.

Anterior shifts in the ventral processing stream locus for face recognition across age as well as the emergence of category-selective activation with increasing age in other brain regions may reflect fine-tuning of visual recognition processes. Other investigations (Gauthier & Nelson, 2001; Passarotti et al., 2003) also support the refinement of visual recognition neural pathways during development. Collectively, these developmental changes may be based on learning and experience.

Maturational shifts in VPS face-preferential loci presented as the primary developmental finding from our experiments in Chapter Four. However, though the location of face-preferential clusters changed with development, the functional activation profiles of face-preferential regions did not change. In children and adults, the face-preferential regions were characterized by differential processing in which faces and other object categories produced significant responses. No category-selective regions emerged in the VPS at any age. A VPS characterized by differential rather than selective processing from childhood to adulthood provided further support for the idea that structural similarity, not taxonomic category, plays a principle role in VPS functional organization.

In addition to our findings, other visual processing studies in impaired and normal adults indicate that structural similarity (SS) processing is a principle force in the organization of the ventral processing stream (VPS) (Arguin et al., 1996; Damasio, 1990; Damasio et al., 1982; Gaffan & Heywood, 1993; Humphreys & Riddoch, 2003; Tranel et al., 1988). However, behavioral data comparing children and adults indicate developmental differences in structural processing (Abecassis et al., 2001; Gibson et al., 1962; Piaget & Inhelder, 1948). Therefore, in Chapter Five, we used fMRI to investigate maturational changes in the functional organization of the VPS relevant to a structural mechanism of object recognition. From existing data, we predicted increased use of structural processing with age.

FMRI and behavioral data were collected during a visual recognition task in which 5-8 year olds, 9-11 year olds, and adults made same/different judgments for shape pairs with parametrically varied levels of SS. Our fMRI findings agree with previous behavioral studies that cite developmental changes visual processing from early school years to adulthood. (Aylward et al., 2005; Carey & Diamond, 1994; Freire & Lee, 2001; Freire & Lee, 2003b; Gathers, Bhatt, Corbly et al., 2004; Mondloch et al., 2002; C.J. Mondloch et al., 2003; Passarotti et al., 2003; Schwarzer, 2000). Though error rates and sensitivity indicate the use of SS processing from 5 years to adulthood, fMRI data do not reveal neural correlates for structural processing until 9-11 years of age. From nine years of age, VPS regions emerge that are sensitive to processing highly structurally similar objects. This potential conflict in behavioral and fMRI results may be attributed to developmental changes in processing strategies. Bias measures indicated that with age criterion settings become more liberal for distinguishing between highly similar objects. These developmental changes in strategy correspond in time to previously identified changes in relational (holistic, configural) vs. featural face processing strategies (Carey & Diamond, 1994). Furthermore, anterior fusiform regions currently identified as sensitive to high structural similarity in 9-11 year olds and adults are similar to regions identified as sensitive to holistic representations in car and face processing (Lerner et al., 2001). Hemispheric findings also support a shift toward relational processing. Taken together, current behavioral and imaging data signify developmental changes in the structural similarity processing of objects which may be linked to greater reliance on relational rather than featural strategies with age. Results suggest that modulation of structural similarity may involve manipulation of relational and featural processing. To test this proposal, future studies should investigate SS manipulation within the category of faces. An experiment manipulating SS within the category of faces would test the idea that faces are at the extreme end of the SS continuum. Use of the same/different matching task design would limit the investigation to perceptual processing, constraining potential top-down influences such as memory and semantics.

In Chapter Five, developmental changes in SS processing occurred in the frontal, parietal, and cerebellar loci as well as in the VPS. Similarly, in Chapter Four, though developmental changes occurred in face and object processing in the VPS, age-related increases in selectivity in other cortical regions were also noted. From these findings, we predicted that normal visual processing involves a network of cortical regions not limited to the VPS, and that these networks narrow in spatial distribution and processing selectivity with age. In Chapter Six, using a whole-brain approach, we quantified and qualified developmental changes in the neural correlates of face and object recognition to investigate our prediction.

Data from the fMRI experiment in Chapter Four were re-evaluated for widespread and regional developmental changes using measures of extent, magnitude, and lateralization of activation. In addition, using activation profiles defined by the logical combination hypothesis testing approach (Joseph et al., 2002), neural substrates were evaluated for cognitive processing changes. As predicted, honing of face and object processing networks occurred across development. As adults recruited fewer but larger regions of activation than children, a pattern of scattered cortical activation in children was replaced with primarily VPS activity in adults. However, contrary to the idea of increasingly category-selective neural substrates with development, changes in extent occurred only for regions of shared object and face processing. FMRI signal strength reflected regional developmental changes rather than systematic changes with age. Across all activation profiles, signal strength decreased with age for frontal regions but increased for age in parietal and VPS regions. Measures of lateralization, revealed more right hemisphere activity in adults than children. Hemispheric changes were not category-specific.

These functional changes correspond to documented anatomical changes. Further investigations using more active rather than passive designs are needed to determine the cognitive developmental basis for functional changes that accompany visual processing. In addition, as MRI studies indicate significant structural changes between adolescence and adulthood (Sowell et al., 2001), an adolescent group should be added to the current design to further delineate functional developmental changes in cortical networks for face and object processing. Continued investigations into the developing functional networks of face and object processing will enhance not only our understanding of typical development but may provide increased understanding of developmental disorders involving atypical face and/ or object processing such as developmental prosopagnosia (Damasio et al., 1982) and autism (Boddaret & Zilbovicius, 2002; Critchley, Daly, Bullmore et al., 2000; Schultz & al., 2000). Furthermore, continued investigations into the development of functional networks in all aspects of cognition will help to bridge the gap in neuroscience between the biological constructs and the behavioral outputs of the brain.

Appendix A. Logical Combination Approach Used in the Current Studies

To test for preferential, selective, graded, and conjoined brain activation patterns or profiles using the logical combination approach, (Joseph et al., 2002) each of the 12 statistical z-maps (group and individual) was thresholded at a z-score of 1.644 corresponding to an uncorrected probability of .05 for a one-tailed test. Thresholded z-maps were then converted into binary masks with any z-score above the threshold assigned the value of 1 and any z-score below the threshold having a value of 0. The binary masks were then combined using logical operators in the image calculator of MEDx to yield 7, unsigned, eight-bit images referred to as voxel-based activation profile masks. (See below for details on how profile masks were created by logical combination of thresholded z-maps). In each profile mask, a voxel was associated with a value of 1 only if it reflected the corresponding profile; otherwise it was given a 0 value. For example, in the profile mask used to isolate regions selectively activated by fixation processing, voxels with the value of 1 were those that showed a statistically greater response to fixation than to any other experimental condition and did not produce a statistically different response among the other conditions (F, N, M). Voxels associated with the value 0 did not have this profile.

Unique combinations of categorical contrasts produced seven voxel-based profile masks: a) face-preferential, b) face-selective, c) manufactured- selective, d.) natural-selective, e.) fix-selective (baseline), f.) face-manufactured-natural graded, and g.) face-manufactured-natural conjoined. Each categorical contrast was represented by a pair of conditions (within parentheses) in which the condition to the left of the '>' sign served as the experimental condition and the condition to the right of the '>' served as the control condition. (The four experimental conditions were face processing (F), manufactured object processing (M), natural object processing (N), and, the baseline, visual fixation (fix).) Categorical contrasts were combined using logical operators (AND = &, OR = |, and NOT = ~).

To isolate voxels with selective responses, the following categorical contrasts were combined: face-selective = [(F>fix) & (F>M) & (F>N)] &~ (M>fix) &~ (M>N) &~ (N>fix) &~ (N>M) &~ (fix>M) &~ (fix>N); manufactured-selective = [(M>fix) & (M>F) & (M>N)] &~ (N>fix) &~ (N>F) &~ (F>fix) &~ (F>N) &~ (fix>N) &~ (fix>F); natural-selective = [(N>fix) &

(N>M) & (N>F)] &~ (M>fix) &~ (M>F) &~ (F>fix) &~ (F>M) &~ (fix>M) &~ (fix>F); fix-selective = [(Fix>M) & (Fix>N) & (Fix>F)] &~ (N>F) &~ (N>M) &~ (M>F) &~ (M>N) &~ (F>M) &~ (F>N).

To isolate voxels with face-preferential responses, used to identify the FFA, the following categorical contrasts were combined: [(F>M)| (F>N)] & (F>fix).

To isolate voxels with face-manufactured-natural graded responses, the following categorical contrasts were combined: [(F>M) & (M>fix)]|[(F>N) & (N>fix)].

To isolate voxels with face-manufactured-natural conjoined responses, the following categorical contrasts were combined: [(F>fix) & (M>fix) & (N>fix)] &~ (F>M) &~ (F>N) &~ (M>F) &~ (M>N) &~ (N>F) &~ (N>M).

Cluster detection was used to eliminate spatially isolated voxels from the voxel-based profile masks by searching each z-map for groups of spatially contiguous voxels above the specified threshold ($z > 2.33$, $p < .05$). The clusters that emerged served as regions-of-interest (ROIs). Repeated-measures ANOVAs were conducted in each of the ROIs to confirm a main effect of condition (F, M, N, fix). Post-hoc comparisons with Bonferroni correction were conducted within each ROI to verify logical combination profiles. To confirm face-selective ROI's, the following contrasts were significant at an alpha level of .008: (F>fix), (F>M), (F>N), and the following contrasts were not significant at the same alpha level: (M>fix), (N>fix), (M>N), and (N>M). Manufactured, natural, and fix-selective ROI's were confirmed at the same alpha level of significance (.008). For manufactured-selective ROI's (M>fix), (M>F), and (M>N) must were significant and (F>fix), (N>fix), (F>N), and (N>F) were not significant. For natural-selective responses the following contrasts were significant (N>fix), (N>F), and (N>M) and not (M>fix), (N>fix), (F>M), and (M>F). Fix-selective profiles were confirmed when (fix>F), (fix>M), and (fix>N) were significant but not (F>M), (F>N), (N>M), and (M>N). To confirm face-preferential ROI's, the following contrasts were significant at an alpha level of .017: (F>fix) and (F>M) or (F>N). ROI's were characterized as face-manufactured-natural-graded profiles when (F>fix), (M>fix), (N>fix), and (F>M) or (F>N) were significant at an alpha level of .017. Face-manufactured-natural conjoined responses were confirmed when the following contrasts were significant at .017: (F>fix), (M>fix), and (N>fix), and (F>N), (F>M), (N>M), (N>F), (M>F), and (M>N) were not significant at the same level.

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Vita

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Education

1992-1995	M.S.	Speech-Language Pathology	University of Louisville, Louisville
1988-1992	B.S.	Biology	University of Tennessee, Martin

Teaching and Training Experience

Teaching

2004, Spring	Unit lecturer for *Anatomy 209*, University of Kentucky
2003, Fall	Guest lecturer for *Anatomy 209*, University of Kentucky
2003, Spring	Teaching assistant for *Medical Neuroanatomy* laboratories, University of Kentucky
1991-1992	Teaching assistant for *Introductory Biology*, *Introductory Zoology*, and *Introductory Botany* laboratories, Department of Biology, University of Tennessee, Martin

Training Courses

2003, Spring	Preparing Future Faculty
2002, Fall	College Teaching

Student Supervising

1997-2000	Clinical supervisor for University of Louisville students in pediatric, early-intervention clinical rotations for speech-language pathology

Research and Training Experience

Research

2001-present	*Graduate Research Fellow*, University of Kentucky, Dr. Jane Joseph, advisor. (859) 323-1825. Experience with Medx, fsl, SPSS, E-Prime, and Excel.

Dissertation Title: *Developmental fMRI Study: Face and Object Recognition*.

Training Courses

2004	Writing, Editing, and Publishing in Science, Society for Neuroscience Annual Conference, San Diego, CA
2003	Professional Skills Workshop, Society for Neuroscience Annual Conference, New Orleans, LA

2002	Grant Writing Workshop, Society for Neuroscience Annual Conference, Orlando, FL
2002	Functional Magnetic Resonance Imaging: An Introductory Course, Medical College of Wisconsin, Milwaukee, WI

Other Work Experience

1996-2000	*Pediatric Speech-Language Pathologist*, Rauch, Inc., New Albany, IN; Amelia Williams, supervisor.
1995-1996	*Speech-Language Pathologist*, Mariner Rehab, Clarksville, IN; Dr. S.A. Larson, supervisor.

Honors and Awards

2004	Commonwealth Research Award
2004	Outstanding Graduate Poster Presenter, University of Kentucky (UK), Neuroscience Day
2003-2005	Ruth L. Kirschstein NRSA Pre-doctoral Fellowship, NIH
2003	Graduate Poster Presenter Award, UK, Neuroscience Day
2003	Eli Lily, SFN Chapters Graduate Student Travel Award
2003	Organization for Human Brain Mapping Travel Award
2002-2003	MRI Spectroscopy Center Pilot Study Grant, UK
2001-2003	Kentucky Opportunities Fellowship, UK
2002	Outstanding Graduate Poster Presenter, UK, Neuroscience Day
2000-2001	Research Challenge Trust Fund I Fellowship, UK
1989-1992	University Scholar Scholarship Award, University of Tennessee, Martin (UT Martin)
1989-1992	Aqua-Knight Adopt-a-Scholar Scholarship, UT Martin
1991-1992	American Association of University Women Award, UT Martin chapter
1992	UT Martin Arts and Science Achievement Award
1988-1989	Honor Seminar Scholarship, UT Martin

Professional Affiliations

2004	Faculty for Undergraduate Neuroscience, Student member
2003-present	Organization for Human Brain Mapping, Student member
2002-present	Society for Neuroscience, Student member
2002-2005	Society for Neuroscience, Student Representative, University of Kentucky
2001-present	Cognitive Neuroscience Society, Student member
1995-present	American Speech-Language and Hearing Association, Member

University/ Community Service

2005, Spring	Science Fair Judge, SCAPA and Glendover School, Lexington, Kentucky
2004, Fall	Neuroscience Presentations, Model Lab School, Richmond, Kentucky
2004, Fall	Brain Facts Fun Days – Lexington Children's Museum and Living Arts and Science Center, Lexington, Kentucky
2004, Spring	Science Fair Judge, Glendover School, Lexington, Kentucky
2002-2005	Graduate Student Representative, University of Kentucky Society for Neuroscience Chapter

2001-2005	Brain Awareness Week Volunteer/Presenter, Lexington and Louisville
2002, Spring	Graduate Mentor of Georgetown College Undergraduates
2004 & 2002	Anatomy and Neurobiology Departmental Employee Award Committee
2001, Spring	Integrated Biomedical Sciences Graduate Student Advisory Committee

Certifications and Professional Licensure

1996-present	ASHA certified speech-language pathologist
1995-present	Speech-Language Pathology license, Indiana
1999-present	Hanen Certification in Speech-Language Pathology
1997-2000	Early-Intervention Speech-Language Pathology Certification, Indiana

Publications

Peer-Reviewed Articles

Joseph, J.E. & **Gathers, A.D.** (2002). Natural and manufactured objects activate the fusiform face area. NeuroReport, 13(7), 935-938.

Joseph, J.E., **Gathers, A.D.**, & Piper, G.A. (2003). Cortical regions for object and letter processing. Cognitive Brain Research, 17, 56-67.

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Gathers, A.D. et al. (2004). Developmental shifts in cortical loci of face and object processing. NeuroReport, 15(10), 1549-1553.

Manuscripts

Gathers, A.D. et al. (In progress). Developmental changes in fMRI measures of extent, magnitude, and lateralization for face and object processing from five years to adulthood.

Joseph, J.E., **Gathers, A.D.**, Liu, X., et al. (In progress). Reverting back to childhood with inverted faces: Neural developmental changes in holistic face processing.

Presentations

Gathers, A.D. (November, 2004). Developmental Dyscalculia: What Neuroscience Adds to Mathematics. University of Tennessee at Martin Mathematics Colloquium, Martin, Tennessee.

Gathers, A.D., et al. (October, 2004). Developmental Changes in Neural Correlates for Upright and Inverted Faces. 34th Annual Conference of the Society for Neuroscience, San Diego, California.

Published Abstracts

Gathers, A.D., Piper, G., Partin, D., & Joseph, J.E. (2001). Prefrontal and parietal involvement in a structurally graded object recognition task. Society For Neuroscience Abstracts, 27, Program No. 849. 14, San Diego, California.

Gathers, A.D. & Joseph, J.E. (2002). FMRI study reveals face processing overlaps with other areas involved in shape processing. Cognitive Neuroscience Society, 9, Program No. B12, San Francisco, California.

Joseph, J. E. & **Gathers**, **A. D.** (2002). fMRI evidence against cortical specialization in the fusiform gyrus for letter and face recognition. Society for Neuroscience Abstracts, 28, Program No. 161.7, Orlando, Florida.

Gathers, A.D. & Joseph, J.E. (2003). A functional MRI investigation of the neural correlates of object and face recognition in children. Organization for Human Brain Mapping, New York, New York.

Gathers, A.D. & Joseph, J.E. (2003). A comparison of visual shape processing in children and adults. Society for Neuroscience Abstracts, 29, Program No. 890.10, New Orleans, Louisiana.

Gathers, A.D., Bhatt, R., & Joseph, J.E. (2004). Face and object processing across development: A structural similarity mechanism. Cognitive Neuroscience Society, 11, Program No. D24, San Francisco, California.

Gathers, A.D., et al. (2004). A developmental fMRI investigation of the neural correlates of object and face recognition. Organization for Human Brain Mapping, Budapest, Hungary.

Corbly, C.R., Blonder, L.X., Curry, T.B., Farley, A.B., **Gathers, A.D.**, et al. (2004). Are brain activation patterns associated with spatial cognition affected by the menstrual cycle? An fMRI study. Society for Neuroscience Abstracts, 30, Program No. 81.14, San Diego, California.

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