NeuroImage 126 (2016) 184–195

Contents lists available at ScienceDirect

NeuroImage

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

Heterogeneous and nonlinear development of human posterior parietal cortex function

Ting-Ting Chang [a,e,*], Arron W.S. Metcalfe [a], Aarthi Padmanabhan [a], Tianwen Chen [a], Vinod Menon [a,b,c,d,*]

[a] Department of Psychiatry & Behavioral Sciences, Stanford University School of Medicine, Stanford, CA, USA
[b] Department of Neurology and Neurological Sciences, Stanford University School of Medicine, Stanford, CA, USA
[c] Program in Neuroscience, Stanford University School of Medicine, Stanford, CA, USA
[d] Symbolic Systems Program, Stanford University School of Medicine, Stanford, CA, USA
[e] Department of Psychology/Research Center for Mind, Brain & Learning, National Chengchi University, Taipei, Taiwan

ARTICLE INFO

Article history:
Received 4 February 2015
Accepted 23 November 2015
Available online 1 December 2015

Keywords:
Cognition
Connectivity
Mental arithmetic
Posterior parietal cortex
Intraparietal sulcus
Supramarginal gyrus
Angular gyrus

ABSTRACT

Human cognitive problem solving skills undergo complex experience-dependent changes from childhood to adulthood, yet most neurodevelopmental research has focused on linear changes with age. Here we challenge this limited view, and investigate spatially heterogeneous and nonlinear neurodevelopmental profiles between childhood, adolescence, and young adulthood, focusing on three cytoarchitectonically distinct posterior parietal cortex (PPC) regions implicated in numerical problem solving: intraparietal sulcus (IPS), angular gyrus (AG), and supramarginal gyrus (SMG). Adolescents demonstrated better behavioral performance relative to children, but their performance was equivalent to that of adults. However, all three groups differed significantly in their profile of activation and connectivity across the PPC subdivisions. Activation in bilateral ventral IPS subdivision IPS-hIP1, along with adjoining anterior AG subdivision, AG-PGa, and the posterior SMG subdivision, SMG-PFm, increased linearly with age, whereas the posterior AG subdivision, AG-PGp, was equally deactivated in all three groups. In contrast, the left anterior SMG subdivision, SMG-PF, showed an inverted U-shaped profile across age groups such that adolescents exhibited greater activation than both children and young adults. Critically, greater SMG-PF activation was correlated with task performance only in adolescents. Furthermore, adolescents showed greater task-related functional connectivity of the SMG-PF with ventro-temporal, anterior temporal and prefrontal cortices, relative to both children and adults. These results suggest that nonlinear up-regulation of SMG-PF and its interconnected functional circuits facilitate adult-level performance in adolescents. Our study provides novel insights into heterogeneous age-related maturation of the PPC underlying cognitive skill acquisition, and further demonstrates how anatomically precise analysis of both linear and nonlinear neurofunctional changes with age is necessary for more fully characterizing cognitive development.

Introduction

Human problem solving skills undergo complex and experience-dependent changes from childhood to adulthood, resulting in more efficient proficiencies over time (Casey et al., 2005; Durston and Casey, 2006). The development of these skills is supported by increasingly specialized functional brain systems (Durston et al., 2006; Kwon et al., 2002; Rivera et al., 2005; Tamm et al., 2002; Uddin et al., 2010b). Much of our understanding of neurocognitive development is based on linear models of age-related changes in which brain activation increases or decreases linearly from childhood to adulthood (Adleman et al., 2002; Kwon et al., 2002; Menon et al., 2005; Ofen et al., 2007; Rivera et al., 2005). While this approach has provided insights into key neurodevelopmental processes, it can also lead to a misleading view of the nature of cognitive skill development (Galvan et al., 2006; Geier et al., 2009; McRae et al., 2012; Van Leijenhorst et al., 2010). Linear models are limited in that they cannot capture unique effects that may occur at specific stages of development (Brenhouse and Andersen, 2011; Geier et al., 2009). Here we investigate fundamental and unaddressed questions regarding linear and nonlinear age-related changes in proficient arithmetic problem solving.

Although the majority of functional brain imaging studies of cognitive skill development have focused on linear models of age-related change (Adleman et al., 2002; Kwon et al., 2002; Menon et al., 2005; Ofen et al., 2007; Rivera et al., 2005), functional imaging studies of emotion and reward processing have provided evidence for an inverted U-shaped pattern of brain activation, characterized by increased activation from childhood to adolescence followed by decreases from adolescence to adulthood (Brenhouse and Andersen, 2011; Galvan et al., 2006; Geier

* Corresponding authors at: 401 Quarry Rd, Stanford University School of Medicine, Stanford, CA 94305, USA.
E-mail addresses: ting620@stanford.edu (T.-T. Chang), menon@stanford.edu (V. Menon).

http://dx.doi.org/10.1016/j.neuroimage.2015.11.053
1053-8119/

et al., 2010; Somerville et al., 2010; Van Leijenhorst et al., 2010). In addition, studies of brain structure reveal that there are nonlinear changes in the brain from childhood to adulthood (Giedd et al., 1999; Gogtay et al., 2004; Lebel and Beaulieu, 2011; Lenroot and Giedd, 2006), suggesting that many aspects of brain development are not linear, and, importantly, highlighting unique periods of change occurring during the transitional period of adolescence. Adolescence is thought to be a paradoxical stage of development when fundamental building blocks of problem solving are established, but functional and structural maturation of the brain is not yet complete (Blakemore, 2012; Luna, 2004). Thus, the overarching goal of the current study is to contrast brain systems underlying cognitive problem solving in children, adolescents, and adults, with a specific focus on linear and non-linear profiles of age-related change and their relation to behavior.

We focus on numerical problem solving, a cognitive domain crucial for academic and professional success as well as quantitative reasoning in everyday life (Butterworth et al., 2011; Geary, 2013; Geary et al., 2013; Richland et al., 2007). Neurocognitive models of numerical problem solving have highlighted a central role of the posterior parietal cortex (PPC) in numerical task performance (Ansari, 2008; Ansari and Dhital, 2006; Arsalidou and Taylor, 2011; Cantlon and Brannon, 2006; Cohen Kadosh et al., 2008; Dehaene et al., 2003; Houde et al., 2010; Menon et al., 2000; Wu et al., 2009). The PPC is a highly heterogeneous structure, encompassing cytoarchitectonic subdivisions (Fig. 1; Caspers et al., 2008; Choi et al., 2006; Scheperjans et al., 2008a,b) that appear to play differential functional roles in numerical problem solving as evidenced by functional magnetic resonance imaging (fMRI) studies (Rosenberg-Lee et al., 2011b; Wu et al., 2009). In the intraparietal sulcus (IPS), brain activity in the more ventral and anterior subdivisions, IPS-hIP2 and IPS-hIP1 (Choi et al., 2006), is associated with representing abstract quantity information (Arsalidou and Taylor, 2011; Cohen Kadosh et al., 2011; Cohen Kadosh et al., 2008; Dehaene et al., 2003). Ventral to the IPS regions are the angular gyrus (AG) and supramarginal gyrus (SMG). Brain activity in the largest subdivision of the dorsal SMG, the SMG-PF (Caspers et al., 2006), has been linked to supporting working memory processes important for manipulating numerical information (Kaufmann et al., 2011; Metcalfe et al., 2013; Silk et al., 2010). Finally, in adults, functional dissociations during arithmetic problem solving have also been demonstrated in the AG. Activity in the anterior AG subdivision, AG-PGa, and the adjoining SMG subdivision, SMG-PFm, is associated with automatized arithmetic problem solving (Dehaene et al., 2003; Grabner et al., 2007; Rosenberg-Lee et al., 2011b), and the posterior AG subdivision, AG-PGp (Caspers et al., 2006), is inversely associated with task difficulty, showing significant deactivation (activation below the resting baseline) as task difficulty increases (Rosenberg-Lee et al., 2011b; Wu et al., 2009). Brain function in the AG-PGp also shows prominent overlap with the PPC node of default mode network (Greicius et al., 2003; Raichle et al., 2001), a system important for internal mental processes including episodic (Cabeza et al., 2012; Cabeza et al., 2008) and semantic memory (Binder and Desai, 2011).

It is currently not known how the function of these heterogeneous subdivisions within the PPC develops and influences task performance. This is an important area to explore, as it has implications for our understanding of cognitive problem solving during critical periods of development. To this end, we used fMRI to investigate brain responses underlying arithmetic problem solving in a large cross-sectional sample of 25 children (ages 7–10), 19 adolescents (ages 13–17), and 26 young adults (ages 19–22). An arithmetic verification task involving subtraction operations allowed us to assess dynamic changes in the functional engagement of individual PPC subdivisions including the IPS, AG, and SMG. We used subtraction problems as they require more effortful use of calculation procedures, manipulation of abstract quantity, and stronger engagement of multiple subdivisions of the PPC than other operations such as addition and multiplication in adults (Chochon et al., 1999; Prado et al., 2011; Rosenberg-Lee et al., 2011b) and children (De Smedt et al., 2011). In order to better characterize the nature of age-related differences in the PPC, we used both linear and quadratic contrasts to highlight areas that demonstrated consistent developmental change across our three age groups, as well as regions that showed unique responses during adolescence.

An important question we address is how functional brain circuits underlying arithmetic problem solving change with age. Previous research has suggested that numerical cognition relies on a distributed set of inter-connected functional circuits within and outside the PPC, including prefrontal cortex (PFC), ventral-occipital temporal cortex (VTOC), anterior temporal cortex (ATC), and insula (Arsalidou and Taylor, 2011; Menon et al., 2014; Rosenberg-Lee et al., 2015; Rosenberg-Lee et al., 2011a; Supekar and Menon, 2012; Uddin et al., 2010a), and that the functional coupling between the PPC and these regions play a critical role during arithmetic tasks (Rosenberg-Lee et al., 2011a; Supekar and Menon, 2012). For example, using fMRI and an arithmetic problem-solving task, one study found that compared to children (7–9 years), young adults (19–22 years) showed stronger functional connectivity and causal interactions between the PPC and the anterior insula (Supekar and Menon, 2012). Another study demonstrated that functional coupling of fronto-parietal circuits in 2nd graders increased after one year of schooling (Rosenberg-Lee et al., 2011a). Finally, there is evidence to suggest that compared to typically developing

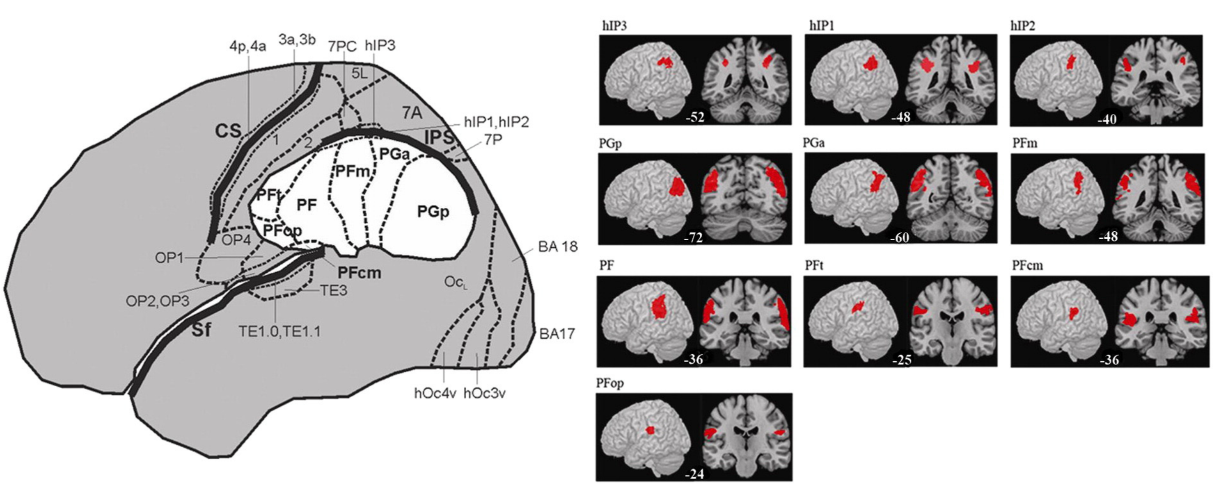

Fig. 1. Cytoarchitectonic maps of posterior parietal cortex (PPC) and its subdivisions. (*Left*) Sagittal view of the PPC regions that are typically activated during arithmetic problem solving tasks, including three intraparietal sulcus (IPS) — hIP3, hIP1, hIP2, two angular gyrus (AG) — PGp and PGa, and five supramarginal gyrus (SMG), PFm, PF, PFt, PFcm, PFop subdivisions. (*Right*) Surface renderings and coronal sections are shown, with the numbers at the bottom of each panel representing the y-axis in MNI coordinates to indicate location of the slices (Adapted from Wu et al., 2009).