Brain and Cognition 92 (2014) 61–72

Contents lists available at ScienceDirect

Brain and Cognition

journal homepage: www.elsevier.com/locate/b&c

Responsiveness and functional connectivity of the scene-sensitive retrosplenial complex in 7–11-year-old children

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ARTICLE INFO

Article history:
Accepted 7 October 2014
Available online 29 October 2014

Keywords:
Attentional modulation
Brain maturation
Functional connectivity
N-back task
Scene-sensitive brain regions

ABSTRACT

Brain imaging studies have identified two cortical areas, the parahippocampal place area (PPA) and the retrosplenial complex (RSC), that respond preferentially to the viewing of scenes. Contrary to the PPA, little is known about the functional maturation and cognitive control of the RSC. Here we used functional magnetic resonance imaging and tasks that required attention to scene (or face) images and suppression of face (or scene) images, respectively, to investigate task-dependent modulation of activity in the RSC and whole-brain functional connectivity (FC) of this area in 7–11-year-old children and young adults. We compared responsiveness of the RSC with that of the PPA. The RSC was selectively activated by scene images in both groups, albeit less than the PPA. Children modulated activity between the tasks similarly in the RSC and PPA, and to the same extent as adults in PPA, whereas adults modulated activity in the RSC less than in PPA. In children, the whole brain FC of the RSC was stronger in the Sf than Fs task between the left RSC and right fusiform gyrus. The between groups comparison suggested stronger FC in children than adults in the Sf task between the right RSC and the left inferior parietal lobule and intraparietal sulcus. Together the results suggest that the function of the RSC and the related networks undergo dynamic changes over the development from 7–11-year-old children to adulthood.

1. Introduction

Top-down attentional control that regulates neuronal activity in sensory cortical areas is important for the ability to selectively attend to behaviourally relevant stimuli and to ignore distracting irrelevant information (Giesbrecht, Weissman, Woldorff, & Mangun, 2006). This regulation is suggested to originate from the prefrontal cortex (PFC) (MacDonald, Cohen, Stenger, & Carter, 2000; Silton et al., 2010) that is intimately involved in higher cognition and shows a protracted maturation. Cognitive processes such as selective attention, working memory (WM) and inhibitory control improve gradually during the course of childhood (Davidson, Amso, Anderson, & Diamond, 2006; Rueda et al., 2004; Vuontela et al., 2003) and the capacity to maintain attention to behaviourally relevant and to ignore irrelevant information increases. Studies of specific perceptual and cognitive functions have examined response patterns in functionally defined category-selective regions in the visual cortex that respond preferentially to objects, faces or scenes (Epstein & Kanwisher, 1998; Kanwisher, McDermott, & Chun, 1997: Malach et al., 1995). Several studies have shown a prolonged maturation for the face-selective cortex (Golarai, Liberman, Yoon, & Grill-Spector, 2010; Golarai et al., 2007; Scherf, Behrmann, Humphreys, & Luna, 2007; Scherf, Luna, Avidan, & Behrmann, 2011) and the emerging face processing network (Cohen Kadosh, Cohen Kadosh, Dick, & Johnson, 2011), and weaker top-down regulation of activity of the fusiform face area (FFA) in children compared to adults (Vuontela et al., 2013). In contrast, less is known about the functional maturation and cognitive control of the place-selective cortex and associated functional networks that support scene-specific perceptual and cognitive processing.

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http://dx.doi.org/10.1016/j.bandc.2014.10.005
0278-2626/

Neuroimaging studies have defined two scene-sensitive brain regions: the parahippocampal place area (PPA) within the posterior parahippocampal and anterior lingual/medial fusiform gyruses (Epstein & Kanwisher, 1998) and the retrosplenial complex (RSC) within the retrosplenial, posterior cingulate, and medial parietal cortex (Epstein, 2008) that is distinct from the anatomically defined retrosplenial cortex (Vogt, Vogt, Perl, & Hof, 2001). These regions are suggested to contribute to different aspects of scene processing (Epstein, 2008); while the PPA supports processing of the physical characteristics of scenes, the RSC is involved in more complex forms of scene-related processing (Epstein & Higgins, 2007; Epstein, Parker, & Feiler, 2007; Park & Chun, 2009).

The PPA is well-described in adult neuroimaging literature (Epstein, 2008; Gazzaley, Cooney, Rissman, & D'Esposito, 2005; Gazzaley et al., 2007; Ranganath, DeGutis, & D'Esposito, 2004; Rissman, Gazzaley, & D'Esposito, 2009). In developmental studies, functional maturation of the PPA has been related to an increase in the volume of this area (Golarai et al., 2007) and to an age-related increase in functional activation during visual scene processing (Chai, Ofen, Jacobs, & Gabrieli, 2010). In these studies, maturational changes in the PPA were associated with improved recognition memory for scene stimuli. Some studies have found differences between children and adults in the function and functional connectivity (FC) of this brain region (Ofen, Chai, Schuil, Whitfield-Gabrieli, & Gabrieli, 2012; Wendelken, Baym, Gazzaley, & Bunge, 2011).

Neuroimaging studies in adults have shown that the responsiveness of the RSC depends on the type of scene processing and on whether the scene stimuli are familiar or unfamiliar (Epstein et al., 2007). Also identification of particular scenes compared to making general judgements of scene category or meaning modify the activity of this area (Epstein & Higgins, 2007). Neuroanatomical (Rushworth, Behrens, & Johansen-Berg, 2006) and resting-state FC studies (Greicius, Supekar, Menon, & Dougherty, 2009; Margulies et al., 2009; Yu et al., 2011) have shown that the retrosplenial cortex is interlinked with several areas of the PFC, cingulate, medial temporal and posterior parietal cortices. Accordingly, the RSC has shown involvement in a range of cognitive functions (Spreng, Mar, & Kim, 2008) including spatial navigation (Epstein, 2008; Maguire, 2001) and memory processes (Summerfield, Hassabis, & Maguire, 2009; Vann, Aggleton, & Maguire, 2009). While these studies have increased understanding of the function of the RSC, top-down regulation of this brain area still remains largely unexplored.

Accumulating evidence from neuroimaging studies has shown that during development maturational changes occur in cortical regions and neural networks that support several domains of complex cognition and perception (reviewed e.g. in Bunge & Wright, 2007; Crone & Dahl, 2012; Luna, Padmanabhan, & O'Hearn, 2010), however, a better understanding of specialization of brain functions during development is still needed. To our knowledge, there are no prior studies in children of the function of the RSC and top-down regulation of activity in this area, or of FC between this and other brain areas. The investigation of the maturation of the RSC and associated functional networks that support scene-specific processing can help to elucidate how more complex forms of visual processing unfold across development.

In our previous study (Vuontela et al., 2013), we used functional magnetic resonance imaging (fMRI) and tasks that required attention to and memorizing of scene (or face) images and suppression of face (or scene) images, respectively, to investigate the function of the PPA and the FFA in 7–11-year-old children. We found that the modulation of activation in the PPA, and FC between the PPA and the PFC, were comparable between 7–11-year-old children and young adults. In the present study, we analyzed further the fMRI data described in our previous study (Vuontela et al., 2013) to investigate the functional maturation of the scene-selective brain region RSC and associated functional networks, and compared the responsiveness of the RSC with that of the PPA. Based on the notion that the RSC, compared to PPA, is involved in more complex scene processing (Epstein, 2008) we hypothesized that the tasks that required selective attention to and memorizing of scene images, might also engage the RSC, but to a lesser extent than the PPA. Furthermore, based on studies that show a protracted development of brain networks involved in complex compared to more basic processing (Gogtay et al., 2004; Jolles, van Buchem, Crone, & Rombouts, 2010; Uddin, Supekar, Ryali, & Menon, 2011), we hypothesized that the function of the RSC and top-down regulation of its activity mature later compared to the PPA and might still be immature in 7–11-year-old children. Developmental studies of resting-state (Fair et al., 2007, 2009; Power, Fair, Schlaggar, & Petersen, 2010; Supekar, Musen, & Menon, 2009) and task-related (Hwang, Velanova, & Luna, 2010) FC have shown that the maturation of functional brain networks involves decreased FC between local and increased connectivity between remote brain areas, and that the behaviour-associated brain networks may undergo dynamic changes during development (Johnson, 2011). Accordingly, we also anticipated that FC during task performance in children may differ from that in adults, and may be stronger between local and weaker between remote brain regions and the RSC. Recent studies, however, have shown that head motion during scanning affects FC analyses and may diminish FC between distant nodes and increase connectivity between local nodes (Satterthwaite et al., 2012; Van Dijk, Sabuncu, & Buckner, 2012). Subject motion is especially critical in developmental studies as children tend to move more during scanning than adults. In the current study, we investigated the FC of the RSC with analysis methods that take into account head movement (Power, Barnes, Snyder, Schlaggar, & Petersen, 2012).

2. Material and methods

2.1. Participants

Eighteen children (aged 7–11 years, 13 males) and thirteen young adults (aged 20–30 years, 7 males) with no prior neurological or psychiatric diseases participated in this study. The child participants were the same as those in the study of Vuontela et al. (2013), in which more details regarding participant demographics were described. Two new adults were included in the present study. Two boys (aged 8 years) were excluded from further analyses due to excessive head movement (>2 mm) during scanning. Thus, a total of 16 children and 13 adults participated in the present study (Table 1). All children and their guardians and all adults gave a written informed consent for the present experimental procedure that was approved by the Ethics Committee for Pediatrics, Adolescent Medicine and Psychiatry at the Helsinki University Central Hospital.

2.2. Tasks and stimuli

The task performed during scanning was a visual 1-back WM task (Vuontela et al., 2013). N-back tasks have been widely used earlier and proven suitable for investigating cognitive processes in school-aged children (Casey et al., 1995; Nelson et al., 2000; Taylor, Donner, & Pang, 2011; Thomas et al., 1999; Vuontela et al., 2003, 2009). The visual stimuli were grey-scale images of natural scenes and faces (Fig. 1A). The season of the scene images and gender of the face images were kept constant within a given block. Each image was shown only once except in match conditions in which the previous image was presented again. Stimuli were 250 pixels wide by 350 pixels tall.