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Neurodevelopmental changes in the responsiveness of systems involved in top down attention and emotional responding

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ABSTRACT

In this study, we aimed to investigate age related changes in systems implicated in top down attention and the implications of this for amygdala responses to emotional distracters. Fifty-one healthy subjects including 18 children (aged 10–14), 15 adolescents (aged 14–18), and 18 young adults (aged 18–25) completed the affective Stroop paradigm while undergoing functional MRI. While achieving comparable behavioral performance, children, relative to adolescents and adults, showed increased activation in areas including anterior cingulate gyrus and precentral gyrus in task relative to view trials. In addition, children showed increased activation within the amygdala and fusiform gyrus in response to emotional stimuli. Notably, the group difference within the amygdala was particularly pronounced during task trials. Also children showed increased connectivity between amygdala and superior frontal gyrus and bilateral postcentral gyrii in response to negative task trials. These data are consistent with previous work indicating less consolidated functional integrity in regions implicated in top down attention in children relative to older participants and extend this work by indicating that this less consolidated functional integrity leads to reduced automatic emotion regulation as a function of top down attention. Given that reduced automatic emotion regulation as a function of top down attention is considered a risk factor for the development of anxiety disorders, these data may contribute to an understanding of the increased risk for the development of these disorders at this age.

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1. Introduction

Dysfunctional emotion regulation is thought to be a risk factor for the development of mood and anxiety conditions (Etkin, Prater, Hoeft, Menon, & Schatzberg, 2010; Rive et al., 2013). However, emotion regulation is a broad term that subsumes a range of cognitive processes (Gyurak, Gross, & Etkin, 2011). Within this range, it has been argued that emotion regulation can engage two sets of control processes (Ochsner & Gross, 2005; Phillips, Drevets, Rauch, & Lane, 2003). The first type of emotion regulation involves ventromedial prefrontal systems that represent emotional value and/or a form of emotional conflict adaptation (Etkin et al., 2010). Some previous developmental work has investigated tasks related to this process: emotional Stroop and emotional go/no-go (Sebastian et al., 2010; Somerville, Hare, & Casey, 2011). These studies have reported increased activation of inferior frontal cortex in children, compared to adolescents and adults, during no-go relative to go trials on a go/no-go task (Somerville et al., 2011) as well as decreased activation of inferior frontal cortex in adolescents relative to adults during performance of the emotional Stroop task (Sebastian et al., 2010).

The second type of emotion regulation involves prefrontal (both dorsomedial and lateral regions) and parietal cortex. Attentional control represents one vital function of these systems: the priming of relevant representations at the expense of irrelevant ones, thereby resolving representational competition (Desimone & Duncan, 1995). Arguably, such control processes can be recruited explicitly within cognitive reappraisal paradigms, where subjects willfully attempt to alter stimulus representations by priming non-emotional features (Ochsner, Bunge, Gross, & Gabrieli, 2002) (see, for reviews, Kalisch (2009) and Ochsner and Gross (2005)). It is argued that these processes are recruited implicitly through attention distraction paradigms (e.g., the affective Stroop task; Blair et al., 2007) where subjects prime task-relevant features of a stimulus array at the expense of the representation of (and consequent emotional reaction to) emotional distracters (Blair et al., 2007; Pessoa, McKenna, Gutierrez, & Ungerleider, 2002; Pessoa, Padmala, & Morland, 2005).

It is the second form of emotion regulation that is of particular interest here. There have been reports that children, relative to adults, show reduced activation in frontal and parietal regions implicated in top down attention (Konrad et al., 2005; Vuontela

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et al., 2013; Wendelken, Baym, Gazzaley, & Bunge, 2011); (for reviews of this literature, see Bunge and Wright (2007), Hwang, Velanova, and Luna (2010) and Rubia (2012)). Similar changes have been observed with respect to working memory and interference control, with age-related improvements in performance and changes in brain activation, particularly in lateral PFC and posterior parietal cortex during task performance being documented (Casey et al., 1995; Hwang et al., 2010; Kwon, Reiss, & Menon, 2002; Olesen, Macoveanu, Tegner, & Klingberg, 2007; Somerville et al., 2011; Velanova, Wheeler, & Luna, 2009). With respect to top down attention driven emotion regulation, the suggestion is that directing attention towards task relevant stimuli will result in reduced representation of emotional distracters and consequent amygdala responses to these distracters (Blair et al., 2007; Pessoa, 2009; Pessoa, Kastner, & Ungerleider, 2002). In other words, if children or adolescents show reduced top down enhancement of task relevant stimuli then it can be predicted that they will show greater emotional (amygdala) responses to emotional distracters. However, this remains to be empirically demonstrated.

Various tasks have been used to index the role of top down attention in the automatic regulation of responding to emotional distracters (dorsomedial and lateral frontal cortices, and inferior parietal cortex; e.g., Blair et al., 2007; Mitchell et al., 2007, 2008; Mitchell, Richell, Leonard, & Blair, 2006; Pessoa, Kastner, et al., 2002; Vythilingam et al., 2007). Here we will concentrate on the affective Stroop task (aST; Blair et al., 2007). In the aST, participants are required to determine the number of numbers presented on the screen. These numbers are temporally bracketed by emotional or neutral distracters. A body of studies with the aST and its variants has shown task performance is associated with increased activity within regions implicated in top down attention (dorsomedial and lateral frontal cortices, and inferior parietal cortex; e.g., Blair et al., 2007; Mitchell et al., 2007, 2008). The amygdala shows responsiveness to emotional relative to neutral distracters and a reduction in this activity in task relative to view trials (where no task performance is required; see Fig. 1; e.g., Blair et al., 2007, 2012; Mitchell et al., 2007, 2008). Importantly, the recruitment of top down attention systems by task demands is not thought to directly inhibit the amygdala. Rather, following Desimone and Duncan (1995), priming of task relevant representations within temporal cortex augments their representation such that the representation of emotional distracters within temporal cortex is suppressed following representational competition. This reduced representation of the emotional distracters results in a reduced amygdala response to these distracters. The aST has been used not only in studies for healthy individuals but also in a series of studies with patients with a variety of anxiety conditions (Social Phobia [SP], Generalized Anxiety Disorder [GAD] and PostTraumatic Stress Disorder [PTSD]; Blair et al., 2012, 2013; Vythilingam et al., 2007). Patients with these conditions show a reduction during task trials in the recruitment of regions implicated in top down attention (dorsomedial [SP, GAD] and lateral frontal and parietal cortices ([SP, GAD, PTSD]); Blair et al., 2012, 2013). Given this evidence that patients with anxiety disorders face difficulty in automatic emotion regulation as a function of top down attention and evidence that children, relative to adults, show reduced recruitment of frontal and parietal regions implicated in top down attention (Bunge & Wright, 2007; Hwang et al., 2010; Rubia, 2012). It is possible that children may show heightened amygdala responses to emotional distracters and that this enhanced responsiveness to emotional task-irrelevant information may contribute to the enhanced risk for the development of anxiety disorders in early adolescence.

In short, we believe this study is the first to examine developmental changes in emotion regulation as a function of top down attention. Specifically, we test two predictions. First, given previous results of reduced recruitment of regions implicated in top down attention (dorsomedial, lateral frontal and parietal cortices) in children and adolescents relative to young adults on tasks requiring top down attention (Konrad et al., 2005; Vuontela et al., 2013; Wendelken et al., 2011), we predict that this will also be seen in the current study during performance of the affective Stroop task. Second, given that priming of task relevant stimulus features via top down attention control is associated with reduced amygdala responses to emotional distracters (Blair et al., 2007; Mitchell et al., 2007), potentially reduced priming of task relevant stimulus features in children/adolescents should be associated with increased amygdala responses to emotional distracters under task conditions. In addition, we examine age related changes in connectivity between the amygdala and cortical regions as a function of task performance.

2. Method

2.1. Subjects

Fifty two healthy participants from the Washington D.C. metropolitan area volunteered for the study and were paid for

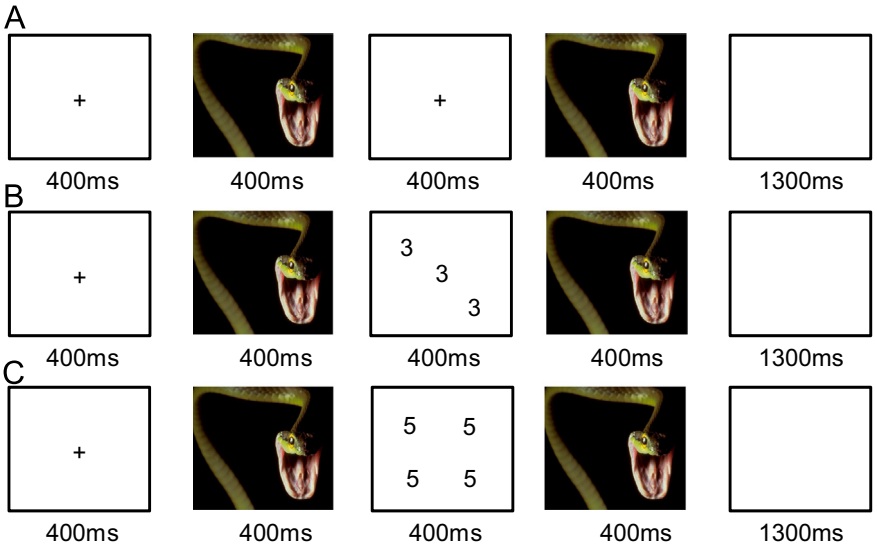

Fig. 1. Example trial sequences. (A) Negative view trial; (B) negative congruent trial; (C) negative incongruent trial.