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Developmental changes in the cortical sources of spontaneous alpha throughout adolescence

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ABSTRACT

This study investigated age-, gender-, and puberty-related changes in two cortical sources of spontaneous alpha during eyes-open and eyes-closed conditions in a cohort of adolescents aged 9–23 years. In total, 29 pre-adolescents (9–12 years, 14 females), 29 mid-adolescents (13–17 years, 14 females), and 33 late adolescents (18–23 years, 17 females) had their resting brain activity measured using electroencephalography (EEG) during eyes-open and eyes-closed conditions. Standardised Low Resolution Brain Electromagnetic Tomography (sLORETA) was used to estimate the cortical sources of spontaneous alpha. Two cortical sources were chosen as regions of interest (ROIs): prefrontal cortex and occipital cortex. Significant age-related changes in the cortical sources of alpha were found, particularly in prefrontal regions; prefrontal alpha power was greater during the eyes-open condition compared to the eyes-closed condition for late adolescents, but equivalent across the eyes-open and eyes-closed conditions for both pre- and mid-adolescents. In addition, more advanced pubertal stage predicted reduced alpha power in male, but not female, adolescents aged 9–17 years. This study provides an important initial step towards understanding developmental changes in the cortical sources of spontaneous alpha in the typically developing brain. Moreover, the results from this study underscore the need to tease out the effects of age, gender, and puberty when examining the cortical sources of alpha during the adolescent period.

1. Introduction

1.1. Adolescent brain development

The human brain undergoes substantial structural changes during adolescence. Structural magnetic resonance imaging (sMRI) studies have consistently documented a decrease in grey matter volume (Giedd, 2004; Gogtay et al., 2004; Mills et al., 2016) and an increase in white matter volume (Barnea-Goraly et al., 2005; Giedd, 2004) throughout the adolescent period. These changes in grey and white matter are thought to reflect the removal of superfluous synapses and their associated neuropil, myelination, and/or increases in axon size (Paus et al., 2001; Sowell et al., 1999; Sowell et al., 2002). These structural changes largely occur in a back-to-front order, with posterior cortical regions maturing earlier in development than anterior cortical regions (Gogtay et al., 2004). There is also evidence that grey matter volume in subcortical structures matures earlier in development than in cortical prefrontal regions (Mills et al., 2014). Thus, compared to other cortical and subcortical regions, the prefrontal cortex (PFC) undergoes a protracted development across adolescence, which extends into the third decade of life (Giedd, 2004; Gogtay et al., 2004; Huttenlocher, 1979; Mills et al., 2016).

Corresponding age-related changes in scalp-recorded electroencephalography (EEG) activity have been widely reported (see Segalowitz et al., 2010 for a review). Overall, studies show that the absolute EEG power decreases with age during childhood and adolescence (Bresnahan et al., 1999; Dustman et al., 1999), and that these decreases coincide with developmental reductions in grey matter volume (Whitford et al., 2007). Moreover, changes in the distribution of EEG activity, where slower activity is replaced with faster activity, begin in occipital cortical regions and progress to frontal cortical regions (Dustman et al., 1999; Gasser et al., 1988a; Gasser et al., 1988b; Matoušek and Petersén, 1973). Consistently, there is also evidence that prefrontal EEG activity continues to mature during late adolescence (Hudspeth and Pribram, 1990). Finally, augmentation of white matter volume during adolescence is thought to result in age-related increases in peak EEG frequency and EEG coherence, and consequently more efficient and faster neuronal communication (Segalowitz et al., 2010).

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1.2. Spontaneous alpha

Spontaneous EEG activity is recorded while participants are awake and resting with their eyes open or closed and measures the endogenous fluctuations of cortical activity. The most dominant spontaneous EEG frequency is alpha (Klimesch, 1999). The alpha rhythm oscillates in the frequency range between 8 and 13 Hz, and has maximal amplitude over occipital regions when individuals are awake and resting with their eyes closed (Berger, 1929). Alpha power is inversely related to cortical activity (Haegens et al., 2011; Shagass, 1972), and studies suggest that individual differences in alpha power are largely determined by genetic factors (Smit et al., 2006; Van Beijsterveldt and Van Baal, 2002). Developmentally, the peak frequency of spontaneous alpha increases from approximately 3 Hz in early infancy to the adult peak frequency of 10 Hz by early adolescence (Lindsley, 1939; Marshall et al., 2002; Niedermeyer, 1997; Somsen et al., 1997; Stroganova et al., 1999). Moreover, spontaneous alpha power decreases across all areas of the scalp during childhood and adolescence (Bresnahan et al., 1999; Dustman et al., 1999). Alpha power is therefore less stable during adolescence than adulthood (Tenke et al., 2018).

EEG studies examining the functional significance of alpha have consistently reported that alpha power is associated with performance on tasks measuring cognitive function (Boiten et al., 1992), memory encoding and retrieval (Klimesch et al., 1997; Vogt et al., 1998), and attention (Cooper et al., 2003; Van Winsun et al., 1984). Moreover, these studies report that alpha synchronises (increases) in task irrelevant cortical areas and desynchronises (decreases) in task relevant cortical areas, and that greater alpha desynchronisation is associated with better task performance (e.g., Klimesch et al., 1997). There is also evidence that alpha power is associated with general intelligence (Alexander et al., 1996; Jaušovec and Jaušovec, 2000) and theory of mind in children (Sabbagh et al., 2009). Repetitive transcranial magnetic stimulation (rTMS) studies also support the idea that alpha is integral to cognitive functioning. For instance, Klimesch et al. (2003) found that rTMS over the frontal and parietal cortices at 1 Hz above participants' individual peak alpha frequency significantly improved cognitive task performance. Taken together, these findings clearly demonstrate that alpha power has an active role in gating relevant and irrelevant brain activity to facilitate efficient neuronal processing and cognitive functioning (Foxe and Snyder, 2011; Jensen et al., 2012; Klimesch, 1999; Klimesch et al., 2007).

1.3. Sources of spontaneous alpha

Scalp-recorded EEG activity represents activity from a number of spatially dispersed cortical and subcortical sources. Thus, the underlying cortical and subcortical sources of spontaneous alpha cannot be determined from scalp-recorded EEG activity. More recent work has therefore aimed to identify the cortical and subcortical sources of spontaneous alpha. To date, the vast majority of studies have investigated the sources of spontaneous alpha in healthy adults with their eyes closed (Cuspineda et al., 2009; de Munck et al., 2007; Feige et al., 2005; Goldman et al., 2002; Lüchinger et al., 2011). Together, these studies provide convincing evidence to suggest that the thalamus and occipital-parietal cortices are the primary sources of spontaneous alpha during eyes-closed conditions. However, several studies have reported that frontal and temporal cortical regions also have a role in generating spontaneous alpha during eyes-closed conditions (Cuspineda et al., 2009; Goldman et al., 2002; Wu et al., 2010). While less work has examined the sources of spontaneous alpha in healthy adults during eyes-open conditions, the initial work suggests that a wider neural network is engaged when the eyes are open compared to when the eyes are closed (Lüchinger et al., 2011). There is also evidence that the shift from eyes-closed to eyes-open significantly reduces the haemodynamic response in the thalamus and across frontal, temporal, parietal and occipital cortical regions (Feige et al., 2005; Wu et al., 2010).

These findings collectively suggest that cortical regions and the thalamus have a role in generating spontaneous alpha during eyes open and eyes closed conditions. It has been reported that the alpha rhythm can be detected slightly earlier in the thalamus than in the cortex (de Munck et al., 2007), suggesting that the thalamus generates the alpha rhythm and subsequently induces synchronised alpha activity in the cortex. However, there is also work to suggest that cortico-cortical networks that are independent of thalamic input generate spontaneous alpha (Lopes da Silva et al., 1980). The evidence to date therefore suggests that spontaneous alpha is generated by a combination of thalamo-cortical and cortico-cortical networks (Başar et al., 1997; Lopes da Silva and Van Leeuwen, 1977; Steriade et al., 1990).

1.4. Age- and gender-related changes in the sources of spontaneous alpha

To the authors' knowledge, only one study has examined age-related changes in the sources of spontaneous alpha during adolescence (Lüchinger et al., 2011). Lüchinger et al. (2011) recorded simultaneous EEG-fMRI in healthy adolescents (15 years) and young adults (25 years) and found that adolescents and young adults had comparable patterns of cortical and subcortical alpha activity during both eyes-open and eyes-closed conditions. While Lüchinger et al.'s (2011) study represents a first step in understanding the sources of spontaneous alpha during adolescence, the sample only included 15 and 25 year olds and thus the findings cannot be generalised to adolescents of other ages. Moreover, Lüchinger et al. (2011) did not explore potential gender differences in the sources of spontaneous alpha. There are significant gender differences in cortical and thalamic grey matter volume during adolescence (see Lenroot and Giedd, 2010 for a review) and grey matter volume tends to peak 1–2 years earlier in development in females than males (Lenroot et al., 2007). Consistently, gender differences have been reported in scalp-recorded EEG resting alpha in children, adolescents, and adults (Barry et al., 2004; Barry and Clarke, 2009; Jaušovec and Jaušovec, 2010). Consequently, additional work is needed to explore potential gender differences in the sources of spontaneous alpha throughout the course of adolescence.

1.5. Puberty-related changes in sources of spontaneous alpha

Puberty is a developmental period encompassing the physical changes that are necessary for sexual maturation (Spear, 2000). The onset of puberty varies markedly between individuals; puberty can begin any time between 8 and 13 years for healthy females and 9–14 years for healthy males (Sørensen et al., 2013). There are an increasing number of studies reporting that pubertal influences contribute to gender differences in cortical grey matter during adolescence (Bramen et al., 2011; Neufang et al., 2008; Peper et al., 2009). Gender differences in thalamic grey matter during adolescence have also been found (Sowell et al., 2002) but, in contrast to cortical grey matter, such differences do not seem to be associated with puberty (Bramen et al., 2011; Peper et al., 2009). Given that alpha is generated by widespread cortical regions in addition to the thalamus (Cuspineda et al., 2009), is possible that the effects of puberty on cortical grey matter development may in turn influence the development of spontaneous alpha. Despite this, no study has yet explored the relationship between puberty and the cortical sources of spontaneous alpha during adolescence.

1.6. The present study

This study aimed to investigate the age-, gender-, and puberty-related changes in the cortical sources of spontaneous alpha in a cohort of adolescents aged 9–23 years. Two cortical sources were chosen as regions of interest (ROIs): the PFC and occipital cortex. The PFC is a cortical source of spontaneous alpha during both eyes-open and eyes-closed conditions (Cuspineda et al., 2009; Lüchinger et al., 2011), and continues to develop structurally (Gogtay et al., 2004; Mills et al.,