Clinical Neurophysiology 127 (2016) 2599–2609

Contents lists available at ScienceDirect

Clinical Neurophysiology

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

Maturation of the P3 and concurrent oscillatory processes during adolescence

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ARTICLE INFO

Article history:
Accepted 23 April 2016
Available online 3 May 2016

Keywords:
Adolescence
Target detection
Brain oscillations
ERP
Post-stimulus amplitude modulation
ITC

HIGHLIGHTS

- Healthy brain development leads to increased precision in timing of event-related neural activation.
- Time–frequency analysis differentiates selective developmental processes underlying the P3.
- Integration of ERPs and brain oscillations provides detailed information about the adolescent brain.

ABSTRACT

Objective: During adolescence event-related modulations of the neural response may increase. For slow event-related components, such as the P3, this developmental change may be masked due to increased amplitude levels of ongoing delta and theta oscillations in adolescents.
Methods: In a cross-sectional study design, EEG was measured in 51 participants between 13 and 24 years. A visual oddball paradigm was used to elicit the P3. Our analysis focused on fronto-parietal activations within the P3 time-window and the concurrent time–frequency characteristics in the delta (~0.5–4 Hz) and theta (~4–7 Hz) band.
Results: The parietal P3 amplitude was similar across the investigated age range, while the amplitude at frontal regions increased with age. The pre-stimulus amplitudes of delta and theta oscillations declined with age, while post-stimulus amplitude enhancement and inter-trial phase coherence increased. These changes affected fronto-parietal electrode sites.
Conclusions: The parietal P3 maximum seemed comparable for adolescents and young adults. Detailed analysis revealed that within the P3 time-window brain maturation during adolescence may lead to reduced spontaneous slow-wave oscillations, increased amplitude modulation and time precision of event-related oscillations, and altered P3 scalp topography.
Significance: Time–frequency analyses may help to distinguish selective neurodevelopmental changes within the P3 time window.

1. Introduction

Developmental trajectories during adolescence may have lasting influence on mental health, social integration and cognitive abilities during adulthood (Kaiser and Gruzelier, 1999; Nuechterlein et al., 2014; Pantelis et al., 2009). Recent studies argue that social and cognitive abilities improve throughout the entire maturational period of life, including adolescence (Amso et al., 2014; Anderson et al., 2001; Blakemore and Choudhury, 2006). An event-related potential measured with the electroencephalogram (EEG), the P3, is suited to investigate maturation of neural processes activated during cognitive tasks (Polich et al., 1990; van Dinteren et al., 2014b). The P3 may comprise superimposed event-related oscillations in different frequency ranges (Demiralp et al., 2001). Although this highlights the importance of investigating changes in brain oscillations during development, studies in this field are still rare (Maguire and Abel, 2013; Segalowitz et al., 2010). The aim of this study was to utilise time–frequency analysis of the P3 to reveal selective neurodevelopmental processes during the transition from adolescence into young adulthood.

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http://dx.doi.org/10.1016/j.clinph.2016.04.019
1388-2457/

1.1. Maturational changes of the P3

Oddball tasks, during which rare and task-relevant targets are randomly dispersed between frequent non-target stimuli, reliably elicit the P3 or P3b (see Fig. 1; Basar-Eroglu et al., 2001). The P3 peaks between 300 to 800 ms, has a posterior maximum (Polich, 2007) and is generated by widespread neural sources comprising frontal and parietal brain regions (Bocquillon et al., 2011; Wronka et al., 2012). The component is reported to play a functional role in attention, memory, decision-making and linking perception with task-relevant action (Basar-Eroglu et al., 1992; Polich, 2007; Twomey et al., 2015; Verleger et al., 2005). Within the P3 time window multiple event-related neural processes may occur (Bledowski et al., 2012; Falkenstein et al., 1994; Galashan et al., 2015); serving more than one specific cognitive function (Mathes et al., 2012; Roman et al., 2005). During oddball paradigms P3 amplitude may reflect target expectancy and P3 latency may reflect processing time (Picton, 1992; Strüber and Polich, 2002).

van Dinteren and colleagues (2014a,b) recently published a meta-analysis and two large multi-centred studies of life-span changes of the auditory oddball P3 during target detection. They reported an increase of P3 amplitude and decrease of P3 latency with age until young adulthood. They showed that the maximum posterior P3 amplitude and the minimum P3 latency are reached early during adulthood, even though the maximum of the P3 amplitude is reached first. Frontal P3 amplitude continues to increase until the 4th decade of life. Taken together, these studies indicate that selective neurodevelopmental changes impact on the P3.

1.2. Reasoning for time–frequency analyses of the P3

Brain oscillations integrate and coordinate neural information processes between segregated, functionally distinct brain areas into a regulated time-flow of activation within neural networks (Basar and Güntekin, 2009; Buzsaki et al., 2013). Time–frequency analyses allow distinction between oscillatory brain responses in different frequency ranges. They further allow characterization of event-related brain oscillations by amplitude, post-stimulus increase or decrease of amplitude, and trial-by-trial consistency[1]. While amplitude of low frequencies declines with age (Barry and Clarke, 2009; Cragg et al., 2011), post-stimulus amplitude modulations and inter-trial phase coherence (ITC) often increase with age (Liu et al., 2014; Müller et al., 2009; Werkle-Bergner et al., 2009).

Superposition of these trends may distort differences between age groups: High amplitudes during baseline may conceal protracted development of increased post-stimulus modulations of the neural response. However, documentation of both, baseline levels as well as task-related amplitude differences may reduce controversial findings (see also Mathes et al., 2016). Fig. 2 visualises how age differences in ERP measures, such as P3 amplitude, may be diminished due to opposing developmental trends of low-frequency amplitude reduction and post-stimulus increase of trial-by-trial consistency of the neural response. Thus, documentation of amplitude, post-stimulus amplitude modulation and ITC of a given frequency band may allow for distinction between selective developmental trajectories of event-related oscillatory processes during brain maturation.

[1] The amplitude reflects the magnitude of local synchronisation of neural firing patterns (Pfurtscheller and Lopes da Silva, 1999), which can also be expressed in post-stimulus modulations with regard to a baseline (that is, post-stimulus increase or decrease of amplitude; Delorme and Makeig, 2004). Single-trial measures of amplitude reflect neural activity without strict time-locking to an event (Herrmann et al., 2014). Inter-trial phase coherence (ITC) measures the similarity in the periodic characteristic (the phase) of the oscillatory response with regard to an event and, therefore, may reflect the stability of a functional network (Yordanova and Kolev, 2009). Group differences in ITC may occur without changes in amplitude modulations (Nanova et al., 2011).

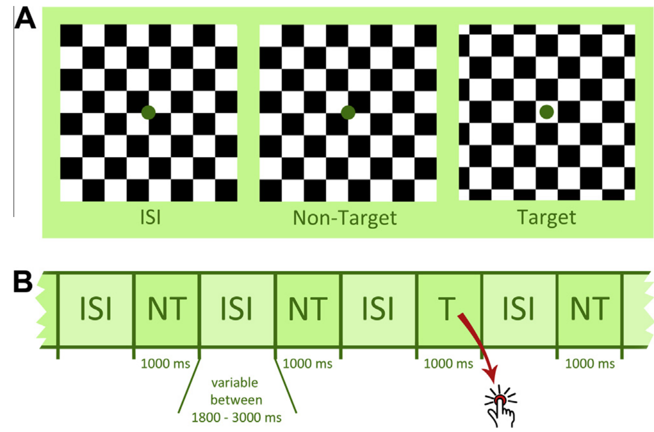

Fig. 1. This schematically illustrates the experimental stimuli (top) and timing (bottom, see methods for further information).

1.3. Maturation of delta and theta oscillations

The shape, topography, timing and amplitude of the P3 seem to be dominated by the superposition of delta (~0.5–4 Hz) and theta (~4–7 Hz) oscillations (Demiralp et al., 2001; Schürmann et al., 1995). Both frequency components have accordingly been linked to reflect similar cognitive processes as the P3 (Basar and Güntekin, 2013; Basar-Eroglu et al., 2001; Mathes et al., 2012).

During tasks requiring cognitive effort, such as target detection, amplitudes of slow event-related oscillations appear to decrease during brain development. However, when taking baseline differences of the oscillatory theta response into account, the developmental pattern reverses: the event-related amplitude modulation with respect to the baseline increases with age (Liu et al., 2014). ITC of event-related delta and theta oscillations also increases with age (Liu et al., 2014; Müller et al., 2009; Papenberg et al., 2013). A recent report showed particularly low ITC of delta oscillations at frontal electrode sites in 10-year-olds (Ehlers et al., 2015). Previous studies on maturation of event-related delta and theta oscillations therefore indicates that in the presence of generally elevated amplitudes, task-related modulations increase with age (Yordanova and Kolev, 2009). This indicates that brain development leads to more precision in timing of neural activation.

1.4. Aim, procedure and hypotheses

We used a visual oddball paradigm, which required detection of rare targets randomly embedded in a stimulus train between frequent non-targets. By analysing the P3, delta, and theta oscillations elicited during this cognitive task we aimed to investigate maturational changes of event-related neural processes during the transition from adolescence into young adulthood.

We hypothesised that while the posterior P3 amplitude may have reached adult levels in adolescents, amplitude differences would still be observed at frontal sites (van Dinteren et al., 2014a,b). Delayed latencies of the P3 might also be observed in adolescents (van Dinteren et al., 2014b). We predicted that pre-stimulus amplitude of delta and theta oscillations would decline (Barry and Clarke, 2009), while post-stimulus modulations in amplitude and ITC would increase during brain development (Müller et al., 2009; Werkle-Bergner et al., 2009; Yordanova and Kolev, 2009).