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Review Article

Electrophysiological changes during adolescence: A review

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ABSTRACT

While psychological research has long shown that adolescence is a period of major cognitive and affective transition, recent neurophysiological research has shown that adolescence is also accompanied by observable maturational changes in the brain, both in terms of structure and neurotransmitter function. Given this situation, we would expect that there should be observable and perhaps major changes in electrocortical activity and responses. In this review, we discuss developmental reductions in EEG power and alterations in the dominant band of EEG oscillation frequency, moderated by developmental factors such as growth-related changes in grey and white matter, and in the developmental history of cognitive and sociocultural stressors. Similarly, we summarize alterations in event-related potential components reflecting stimulus processing, response monitoring, and response anticipation. We review the literature on such changes in EEG and event-related potentials during the adolescent period and summarize some of the new developments in the field as well as interpretative difficulties.

1. Introduction

Adolescence is a time of observable cognitive and emotional change that is reflected in impressive intellectual advances. This transition from childhood to adulthood is accompanied by substantial but less observable internal change, including cerebral maturation. Numerous investigations have focused on the pronounced neurodevelopment and neural reorganization that takes place during adolescence, reflecting both structural and functional changes (see papers in this issue). This paper presents a brief overview of developmental electrocortical changes during adolescence focusing on the two traditions in this field – the electroencephalogram (EEG) and the event-related potential (ERP). While measures of EEG are taken from *continuous* scalp-recorded electrical activity of the brain, the ERP is derived from averaging the EEG signal time-locked to specific events, such as the presentation of stimuli. Maturation of the EEG is most often used as a marker for changes in structural factors, such as the changes in grey and white matter that occur during development. In contrast, ERP changes over age are usually taken as reflections of functional factors in the processing of information, such as changes in attention, working memory, or processing strategy. However, it certainly is reasonable to assume that there are structural changes with age that alter the shape or amplitude of ERP components, and it is often not possible to separate these two sources of alteration in the ERP. Furthermore, it may be difficult to separate these two sources of developmental change: alterations in information processing capacity reflected in the ERP may be as much due to structural maturation of the cortex as to changes in cognitive strategies or skills, because structural changes may affect information processing so as to affect cognitive processing of stimuli, dramatically altering ERP responses. There are several examples of this structural–functional interplay, which we discuss throughout this review. We return to several specific issues in the last section, including that maturation may alter the degree of latency jitter, the affective response the participant has to the task, and age-dependent performance factors, all of which would alter information processing and therefore the ERP.

2. Electroencephalogram (EEG) overview

The spontaneous brain electrical activity measured through the use of scalp EEG reflects the summated activity of postsynaptic cortical pyramidal cells that vary in orientation; voltage will increase or decrease depending on the number of measurable neurons firing together (Lopes da Silva, 2005a). One primary advantage of this technology is its ability to measure dynamically changing cortical processing in real time, making it amenable to the study of ongoing fluctuations in spontaneous brain activity and to changes in brain activity during the processing of specific stimuli, e.g., through the measurement of event-related potentials (ERPs). Spontaneous EEG activity is generally recorded while participants sit quietly in a relaxed state with their eyes closed. The EEG signal, which is the summation of multiple electrical oscillations (sinusoidal rhythms) at different frequencies, is submitted

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to spectral analysis to derive power (which can be thought of as the area under the curve in the EEG scalp recording, and is related to the amplitude of the signal during a specified period of oscillations) in each component frequency band (Lopes da Silva, 2005b). The origin of these oscillations is a matter of continued debate, although thalamo-cortical reciprocal pathways under the control of brainstem and forebrain modulation are strongly implicated in the generation and synchronization of these oscillations (Steriade, 2005).

Component frequency bands are generally described in terms of amplitude (determined by voltage), frequency, topography and functional state (for a review of normal adults' EEG, see Niedermeyer, 2005). The classic five broad bands for the adult EEG include *delta* (0–3 Hz), *theta* (4–7 Hz), *alpha* (8–12 Hz), *beta* (13–30 Hz), and *gamma* (above 30 Hz). Delta and theta oscillations are generally distributed widely across the scalp and are often grouped together in the literature as slow wave activity. Slow wave activity is most prominently observed when individuals are in transition from wakefulness to sleep or during sleep stages, although such activity is also observed during awake states. Alpha oscillations are most prominent in posterior regions and are typically observed when individuals are in a relaxed waking state, while beta oscillations are observed primarily over frontal and central regions while subjects are alert and actively processing information. Gamma band responses have been related to perception and consciousness and are generally observed over frontal regions; however, care needs to be taken that the gamma is not reflecting electromyogram activity from muscle innervations (see Yuval-Greenberg, Tomer, Keren, Nelken, & Deouell, 2008). In some studies, the definitions of beta and gamma overlap or these bands are merged. Several standard EEG measures are typically computed across studies. These include *absolute power* (sum of power for a particular band), *total power* (sum of absolute power across all bands), *relative power* (absolute power for band/ sum of absolute power for all bands), and *asymmetry* (the relative difference in power across hemispheres for a particular region and for a particular band).

2.1. Structural brain changes during adolescence relating to EEG

Although the human brain reaches adult size by about 12 years of age (Caviness, Kennedy, Bates, & Makris, 1996; Dekaban, 1978; Reiss, Abrams, Singer, Ross, & Denckla, 1996), there are a number of structural changes that take place across adolescence and into young adulthood, which may be important when interpreting maturational changes in EEG activity. Given these changes, along with the evidence of major changes in cortical function over the adolescent period (for a review, see Spear, 2003), it is hard to imagine how electrical signal transmission in the cortex could avoid being affected. One highly replicated finding is a substantial decline in grey matter volume, which is thought to be related to the process of "synaptic pruning" or the elimination of synapses and their associated neuropil (dendrites, dendritic spines, axon terminals and possibly associated glia – see Paus, Keshavan, & Giedd, 2008). Cross-sectional MRI studies of normally developing children and young adults have reported that when total brain size is controlled for, grey matter volume declines with age but then stabilizes in adolescence and adulthood (Jernigan, Hesselink, Sowell, & Tallal, 1991; Pfefferbaum et al., 1994; Sowell, Trauner, Gamst, & Jernigan, 2002; Steen, Ogg, Reddick, & Kingsley, 1997). Insomuch as EEG power reflects the summation of pyramidal neuronal activity (Davidson, Jackson, & Larson, 2000), reductions in grey matter volume resulting from synaptic pruning over adolescence should result in reductions of EEG power over the same period. Indeed, absolute EEG power declines with age over adolescence and coincides with grey matter volume reduction (Whitford et al., 2007). MRI studies have also revealed characteristic temporal patterns of regional grey matter reduction over childhood and adolescence (Giedd, 2004; Giedd et al., 1999; Gogtay et al., 2004; Jernigan et al., 1991; Sowell & Jernigan, 1998; Sowell et al., 2002).

Neurophysiological studies suggest that regions involved in basic sensory and motor functions mature earlier (~4–8 years) than areas of the parietal lobe involved in spatial orientation, language and attention (~11–13 years). The last regions to mature are the higher-order areas that integrate basic functions, i.e., heteromodal association areas (Mesulam, 1985). MRI studies have shown that anterior and superior regions of the frontal cortex are some of the last regions to mature, between 12 and 30 years of age (Paus et al., 1999; Sowell, Thompson, Holmes, Jernigan, & Toga, 1999; Sowell et al., 1999). Maturational patterns of EEG activity should parallel regional patterns of grey matter reduction over this period, and in fact there is a redistribution of relative EEG power as a function of age with posterior regions maturing earlier than anterior regions; slower activity (e.g., theta) is replaced by faster activity (e.g. alpha) first in occipital regions and progressing later to frontal regions (Dustman, Shearer, & Emmerson, 1999; Gasser, Jennen-Steinmetz, Sroka, Verleger, & Mocks, 1988; Matousek & Petersen, 1973b). Moreover, there is a "frontalization", where despite reduced overall activity (Yurgelun-Todd & Killgore, 2006), the frontal regions activate to tasks requiring executive functions more in adults than children (e.g., Bunge, Dudukovic, Thomason, Vaidya, & Gabrieli, 2002). Further evidence for a possible relation between EEG power and grey matter volume comes from an extensive study by Boord, Rennie, and Williams (2007). Results from this study show that reductions in estimated cerebral metabolic rate (CMR) co-varied linearly with declines in slow-wave power over the age-span and that these relations are strongest for the subjects under 20 years of age.

Another well-documented structural change during adolescence is the relatively linear increase in white matter volume across all regions (Giedd, 2004; Giedd et al., 1999). Volumetric white matter changes are thought to reflect either the process of increased myelination, an important aspect of cerebral maturation involving the wrapping of neuronal axons in lipid sheaths which greatly increases the speed of neuronal firing (Giedd, 2004) and/ or an increase in axon size (see Paus, 2010). In either case, the result should be an increase in neuronal communication and speed of functioning, both of which have implications for EEG and ERPs, such as increases in peak oscillation frequency, EEG coherence, and ERP speed. Increases in speed of neuronal processing that accompany increased myelination would be expected to facilitate cognitive processing. Indeed, regional white matter maturation has been related to increased cognitive abilities (e.g., reading and memory skills) in children between the ages of 8 and 18 (Nagy, Westerberg, & Klingberg, 2004).

2.2. Developmental change in the EEG

The use of electroencephalogram technology to measure changes across development has a long and rich history. Since Berger's (1929, 1932) original demonstration of age-related changes in infant, child, and adult EEG, numerous studies have collected normative developmental EEG data in an attempt to better understand the boundaries between normality and abnormality. Before the advent of modern computerized technologies, early developmental studies used laborious visual analysis for both longitudinal (Lindsley, 1938; Smith, 1938a; Smith, 1938b) and cross-sectional (Eeg-Olofsson, 1971; Petersen & Eeg-Olofsson, 1971) studies of children, adolescents, and adults (for a comprehensive review of these classic studies see Petersen, Sellden, & Eeg-Olofsson, 1975). These studies and later replications using computer-aided quantitative methods (e.g., Alvarez Amador et al., 1989; John, Prichep, Fridman, & Easton,