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Dissociation of preparatory attention and response monitoring maturation during adolescence

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HIGHLIGHTS

- EEG markers of preparatory attention reflect development, but anterior scalp markers seen in adults are not present even in the older youth.
- EEG markers of response monitoring reflect development.
- Age-related changes in EEG markers of preparatory attention and response monitoring are correlated with age-related changes in performance accuracy.

ABSTRACT

Objective: Substantial brain development occurs during adolescence providing the foundation for functional advancement from stimulus-bound "bottom-up" to more mature executive-driven "top-down" processing strategies. The objective was to assess development of EEG markers of these strategies and their role in both preparatory attention (contingent negative variation, CNV) and response monitoring (Error Related Negativity, ERN, and Correct Related Negativity, CRN).
Methods: CNV, ERN and CRN were assessed in 38 adolescents (18 girls), age 11–18 years, using a variation of a letter discrimination task.
Results: Accuracy increased with age and developmental stage. Younger adolescents used a posterior attention network involved in inhibiting irrelevant information. Activity in this juvenile network, as indexed by a posteriorly-biased CNV and CRN decreased with age and advancing pubertal development. Although enhanced frontal CNV, known to be predictive of accuracy in adults, was not detected even in the older adolescents, top-down medial frontal response monitoring processes (ERN) showed evidence of development within the age-range studied.
Conclusions: The data revealed a dissociation of developmental progress, marked by relatively delayed onset of frontal preparatory attention relative to error monitoring.
Significance: This dissociation may render adolescents vulnerable to excessive risk-taking and disinhibited behavior imposed by asynchronous development of component cognitive control processes.

1. Introduction

The adolescent brain undergoes dramatic maturational changes (Bava and Tapert, 2010; Giedd et al., 2010; Paus, 2010; Schmithorst and Yuan, 2010), with a curvilinear developmental trajectory of brain growth in childhood, followed by a rapid decline in adolescence (Giedd, 2004; Jernigan et al., 1991; Sowell et al., 2002; Steen et al., 1997) (for review, Stiles and Jernigan, 2010). Longitudinal studies reveal regionally specific nonlinear prepubertal increases, followed by post-pubertal decreases in cortical gray matter volume starting in more dorsal parietal cortices, spreading rostrally over the frontal cortex, and ending with the dorsolateral prefrontal cortex (Brain Development Cooperative Group, 2012; Giedd et al., 1999a; Lenroot et al., 2007; Raznahan et al., 2011a,b; Shaw et al., 2008; Sowell et al., 2004; Sullivan et al., 2011). Adolescence is also

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associated with ongoing myelination of neuronal axons, progressing from inferior to superior and from posterior to anterior brain regions (Yakovlev and Lecours, 1967), with a consequent increase in white matter volume determining ultimate brain size (Courchesne et al., 2000; Giedd et al., 1999b; Pfefferbaum et al., 1994; Reiss et al., 1996; Sowell et al., 2004). Thus, brain structures follow different courses of maturation, thereby contributing to different maturational time courses of brain functions. Complex processes that rely on synergistic functions that do not mature in lock-step might help define the "awkward teenager," embodying cognitive mature, maturing, and immature processes. Behavioral challenges incorporating complex attentional tasks measured with electrophysiological probes could serve to identify dissociable functions, index their maturational levels, and provide insight into limitations imposed by asynchronous development of component cognitive processes.

Functional correlates of brain developmental changes are the maturation of cognitive processes in adolescence and a notable shift in strategy from a posterior bottom-up stimulus-driven orienting network of brain regions (Posner and Petersen, 1990) characteristic of immature attentional processes to engagement of an anterior executive top-down attentional network (Corbetta and Shulman, 2002; Posner and Petersen, 1990). Several studies have provided evidence that with advancing adolescence, top-down processing predominates in several domains, including visual search (Acik et al., 2010; Donnelly et al., 2007), phonological processing (Bitan et al., 2009), dichotic listening (Andersson et al., 2008; Takio et al., 2009), and dual processing of verbal and visual information (Karatekin, 2004). Evidence from studies evaluating the effect of working memory load on Stroop interference (Spronk and Jonkman, 2012) and voluntary control of reflex responses (antisaccade task) (Luna et al., 2001) show evidence of effective top-down modulation as not occurring until adulthood. Later development of frontal top-down mechanisms relative to other brain-behavior associations has been hypothesized to underlie the particular vulnerability of adolescents to engage in risky behavior (Casey and Jones, 2010).

Efficient cognitive processing involves both preparatory attention and the continuous monitoring of performance. These control processes permit high levels of functioning and enable flexible actions in response to moment-to-moment changes in the environment. In adults, these processes depend on the integrity of anterior cingulate cortex (ACC) and related prefrontal neural circuitry (Gehring and Knight, 2000; Rosahl and Knight, 1995). Preparatory attention can involve both bottom-up and top-down processing and can be indexed using the EEG waveform, contingent negative variation (CNV). The late phase of the CNV indexes cortical activity specific to preparatory processes involved in the analysis of an imperative stimulus and selection of the appropriate response (Hillyard, 1969; Hillyard et al., 1973). Motor preparation is also related to the CNV. One index of motor preparation that may be superposed onto the CNV is the pre-response lateralized readiness potential (LRP) that is modulated by response conflict (Mathalon et al., 2002). The CNV is most likely the result of activation of a network of prefrontal and parietal association cortices active in judgment and decision making process (Drake et al., 1997; Lai et al., 1997). The dorsolateral prefrontal cortex (DLPFC) is also implicated in CNV generation (Rosahl and Knight, 1995), given that neuronal populations in DLPFC (associated with top-down processing) form recurrent circuits with posterior polymodal association cortices (related to short-term memory and sensory attention bottom-up processes) and premotor areas (Fuster, 2000, 2002). In adults, accuracy in a complex task is predicted by fronto-central CNV amplitude, with correct trials associated with larger, more negative, CNV amplitudes than to error trials (Padilla et al., 2006). Likewise, larger LRP amplitudes may reflect a strategic emphasis on accuracy (versus speed) through an enhancement of response criteria (Wild-Wall et al., 2008).

Evidence for the maturational timeline of the CNV is inconsistent. Early reports indicated that although the amplitude of the CNV was greater in children than adults (Low et al., 1965), age-related changes may cease by age 12 (Low et al., 1966), the age at which Bender et al. (2005) reported stabilization of late CNV topography. A second group, which studied children 6–18 years of age, reported increasing CNV amplitudes at the vertex until age 15 (Tecce, 1971). Studies specifically evaluating the late CNV have reported a linear increase in late CNV with age when comparing 6–7 year-olds, 9–10 year-olds, and 19–23 year-olds (Jonkman, 2006), consistent with another study reporting increasing late CNV in 7–17 year-olds (Segalowitz and Davies, 2004).

Performance monitoring also involves bottom-up and top-down processing. Top-down processing is associated with the Error Related Negativity (ERN), a fronto-central maximal electrophysiological marker observed following an incorrect response (Falkenstein et al., 1991; Gehring, 1993; Gehring and Fencsik, 2001; Gehring and Taylor, 2004; Gehring and Willoughby, 2002). Larger ERNs occur with fast-acting systems that inhibit and correct an error as it occurs and with slower acting systems that prolong reaction time (RT) on trials following errors (Gehring, 1993). A second component occurring with much the same latency as ERN is observed during performance monitoring of correct trials that have high levels of response conflict (Vidal et al., 2000). This Correct Related Negativity (CRN) (Carter et al., 1998; Gehring and Fencsik, 2001) reflects a more basic element of conflict following responses than the ERN. Together, the ERN and CRN comprise markers reflecting different constellations of component processes (Bartholow et al., 2005; Luu et al., 2000; Taylor et al., 2007; van Veen and Carter, 2006). Given that greater accuracy in a complex task has been related to less negative CRN amplitudes in healthy adults (Padilla et al., 2011), it is possible that the CRN is more reflective of bottom-up processing, than the top-down ERN (Kenemans and Kahkonen, 2011).

ERN and CRN appear also to have different developmental trajectories. Several studies report greater ERN amplitude with older age across adolescence (Davies et al., 2004; Ladouceur et al., 2004, 2007; Santesso and Segalowitz, 2008; Segalowitz and Davies, 2004; Wiersema et al., 2007). By contrast, CRN amplitudes have been shown to decrease (i.e., less negative) from 7 to 18 years (Davies et al., 2004).

Thus, developmental trajectories have been estimated for both the preparatory attention-related CNV and the performance monitoring ERP components, the ERN and CRN. Both also show evidence of a shift from bottom-up to top-down processing during adolescence and into adulthood but may mature at different rates. To date, however, there have been no studies evaluating both processes in the same subjects that would permit an evaluation of the relative timing of the development of each set of processes and how they might inter-relate to support efficient cognitive performance. In this cross-sectional study, we examined differences in preparatory attention and response monitoring across adolescence, from age 11 to 18 years, by using a letter discrimination variation of the Eriksen flanker task (Eriksen and Eriksen, 1974; Gehring and Knight, 2000; Padilla et al., 2006). Fronto-central CNV associated with enhanced performance was observed in adults (mean age = 24 years) (Padilla et al., 2006). Based on this observation we tested the hypothesis that larger CNV amplitudes would occur with older adolescence over fronto-central scalp areas and smaller amplitudes over posterior scalp areas. To confirm previous developmental findings, we also tested the hypothesis that larger ERN and smaller CRN amplitude would occur with older age. An additional goal of this study was to examine the relation between response monitoring and preparatory attention potentials.