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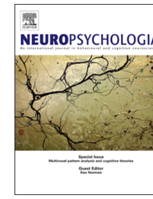

Electrophysiological correlates of attention networks in childhood and early adulthood

Q1 Alicia Abundis-Gutiérrez, Purificación Checa, Concepción Castellanos, M. Rosario Rueda*

Department of Experimental Psychology and Center for Research in Mind, Brain and Behavior (CIMCYC), University of Granada, Campus de Cartuja s/n, 18071 Granada, Spain

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ABSTRACT

Attention has been related to functions of alerting, orienting, and executive control, which are associated with distinct brain networks. This study aimed at understanding the neural mechanisms underlying the development of attention functions during childhood. A total of 46 healthy 4–13-year-old children and 15 adults performed an adapted version of the Attention Network Task (ANT) while brain activation was registered with a high-density EEG system. Performance of the ANT revealed changes in the efficiency of attention networks across ages. While no differences were observed on the alerting score, both orienting and executive attention scores showed a more protracted developmental curve. Further, age-related differences in brain activity were mostly observed in early ERP components. Young children had poorer early processing of warning cues compared to 10–13-year-olds and adults, as shown by an immature auditory-evoked potential complex elicited by warning tones. Also, 4–6-year-olds exhibited a poorer processing of orienting cues as indexed by lack of modulation of the N1. Finally, flanker congruency produced earlier modulation of ERPs amplitude with age. Flanker congruency effects were delayed and more anteriorly distributed for young children, compared to adults who showed a clear modulation of the N2 in fronto-parietal channels. Additionally, interactions among attention networks were examined. Both alerting and orienting conditions modulated the effectiveness of conflict processing by the executive attention network. The Orienting × Executive networks interactions was only observed after about age 7. Results are informative of the neural correlates of the development of attention networks in childhood.

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1. Introduction

Attention serves as a basic set of mechanisms that underlie our awareness of the world and the voluntary regulation of thoughts
Q8 and feelings (Posner et al., 2007). In the past decades, Posner and colleagues (see Petersen & Posner, 2012; Posner & Petersen, 1990) have developed a neurocognitive model of attention, in which three differential neural networks and neuromodulators are assumed to subserve different functions. The alerting network serves the function of reaching and maintaining the state of alertness. It has been associated with frontal and parietal regions of the right hemisphere for sustained or tonic alertness, and the left hemisphere in conditions in which the level of alertness is increased by warning cues (Bekker, Kenemans, & Verbaten, 2004; Coull, Frith, Büchel, & Nobre, 2000). The orienting network is involved in shifting attention and selecting sensory events for preferential processing. This network comprises a number of frontal and parietal structures, such as the superior parietal lobe, the temporal–parietal junction, the frontal eye fields and ventral frontal cortex that are differentially involved in top-down and bottom-up control of attention (Corbetta & Shulman, 2002). Finally, the executive attention network is involved in control processes, such as conflict monitoring, error detection and response selection when competing alternatives are available. The anterior cingulate cortex is the main node of this network (Posner et al., 2007), which also includes areas of the lateral prefrontal cortex.

Within the framework of Posner's model of attention, an experimental paradigm, the Attention Network Task (ANT), was developed several years ago with the purpose of measuring functional efficiency of each attention network (Fan, McCandliss, Sommer, Raz, & Posner, 2002). This task combines presentation of orienting and alerting cues (Posner, 1980) with a flanker-type task (Eriksen & Eriksen, 1974) in order to measure alerting, orienting, and executive attention by means of time and accuracy of responses. Alerting is measured by comparing RT/Accuracy in trials with and without warning cues. Orienting of attention is examined by comparing trials with cues that direct attention to a

* Corresponding author. Tel.: +34 958249609.
E-mail address: rorueda@ugr.es (M. Rosario Rueda).

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location where the target will appear later on (valid cues) to trials without such cues. And, finally, executive attention is measured by comparing trials in which the target is surrounded by congruent flankers to trials with incongruent flankers. Since it was developed, the ANT has been utilized in many studies in order to characterize attention function with a wide variety of populations (e.g. Fan, Wu, Fossella, & Posner, 2001; Jennings, Dagenbach, Engle, & Funke, 2007; Posner et al., 2002; Rueda, Fan et al., 2004). The ANT has also been adapted to children as young as 4 years of age and some cross-sectional studies have been conducted in order to study the development of attention networks during childhood (Mezzacappa, 2004; Rueda, Fan et al., 2004; Rueda, Posner et al., 2004).

While the three functions of attention are thought to be present to some degree by the end of the first year of life, they appear to have differential developmental courses throughout childhood and adolescence (Rueda, 2013, chap. 15). Developmental studies addressing alertness have shown that children have greater difficulty processing warning signals compared to adults (Mezzacappa, 2004; Rueda, Fan et al., 2004). Evidence shows that young children (i.e. 5 years old) need longer warning-to-target intervals in order to benefit from warning cues and are less able to sustain alertness over time compared to older children and adults (Berger & Posner, 2000; Morrison, 1982). On the other hand, children show a progressive increase in orienting speed to valid orienting cues during childhood (Schul, Townsend, & Stiles, 2003). Several studies have shown that the ability to orient attention by means of peripheral as well as central cues seems to reach full maturation by age 10–11 years (Goldberg, Maurer, & Lewis, 2001; Waszak, Li, & Hommel, 2010). However, somewhat longer developmental courses have been observed when disengagement from an invalid location and reorienting to the valid one is needed, particularly under endogenous orienting conditions, as when long intervals between cue and target are utilized (Schul et al., 2003; Wainwright & Bryson, 2005). Finally, there is much evidence that young children experience more difficulty than older children and adults performing tasks that involve conflict. Executive control is often measured using experimental paradigms involving conflict among stimuli, responses, or stimulus-to-response mapping, such as the flanker and Stroop-like tasks. Using a flanker task adapted to children, Rueda and colleagues have reported a significant development of the ability to suppress interference from distracting stimulation during preschool years (Rueda, Fan et al., 2004; Rueda, Posner, & Rothbart, 2005). However, in contrast to the other attention networks, executive attention appears to develop more gradually during childhood and adolescence. Waszak et al. (2010) found that even 14–15-year olds show larger flanker interference than adults, indicating a protracted development of mechanisms related to executive control.

Numerous studies have used event-related potentials (ERP) to examine the neural basis of alerting, orienting and executive attention (see Posner, Rueda, & Kanske, 2007), but a smaller number have addressed neural mechanisms underlying the development of these functions.

Auditory signals are frequently used to study alertness. Commonly, a series of evoked potentials can be recorded from as soon as 10 ms after the presentation of auditory signals (Picton, Hillyard, Krausz, & Galambos, 1974). From about 50 to 250 ms following the tone, a midline-distributed series of component with different polarity (i.e., P1, N1 and P2) can be observed, which has been associated with early attentional preparation, reflecting automatic sensory activation/orientation processes (Bekker et al., 2004; Jonkman, 2006). Alerting cues also elicit a slow negative electrical brain wave, called the contingent negative variation (CNV), occurring at the interval between presentation of the cue and the imperative stimulus (Walter, Cooper, Aldridge, McCallum, & Winter, 1964). The CNV is considered an index of the endogenous maintenance of attentional effort during the expectancy period between the warning cue and the target (Brunia & Damen, 1988; Gómez, Vaquero, & Vázquez-Marrufo, 2004), and seems to have two differentiated phases. The early CNV, which emerges around 300–400 ms after the warning cue, appears to be related to stimulus orientation and task anticipation processes. With cue–target intervals of more than a second, a late CNV component has also been observed, which occurs prior to the imperative stimulus, and is thought to reflect motor preparation (Loveless & Sanford, 1974).

Developmental studies have observed no differences in the modulation of early ERP components by warning cues from age 6 to adulthood (Jonkman, 2006). However, several studies using different tasks have shown that the amplitude of the CNV increases with age (Hämmerer, Li, Müller, & Lindenberger, 2010; Jonkman, 2006; Jonkman, Lansbergen, & Stauder, 2003; Segalowitz & Davies, 2004). Using auditory cues and targets, Bender, Weisbrod, Bornfleth, Resch, and Oelkers-Ax (2005) found that 6–12-year-old children elicited the early CNV component but not the motor component of the CNV, which was only observed for children aged 12 years and adults.

With respect to orienting of attention, studies with adults have reported that visual targets preceded by valid spatial cues elicit brain potentials of enhanced amplitude over occipital leads, in comparison to targets presented at uncued locations (Curran, Hills, Patterson, & Strauss, 2001; Lorenzo-López et al., 2002; Mangun, Hansen, & Hillyard, 1986; Mangun & Hillyard, 1991). Generally, increased P1 and reduced posterior P3 amplitudes are obtained in validly cued trials with respect to invalid ones. Modulation of the P1 is related to facilitation of early sensory processing by attention (Hawking et al., 1990; Mangun & Hillyard, 1987). On the other hand, modulation of the P3 has been related to stimulus evaluation processes. The higher amplitude of the P3 for invalidly cued trials appears to signal a mismatch between sensory perception and sensory-motor preparation (Digiacomo, Marco-Pallarés, Flores, & Gómez, 2008; Gómez, Flores, Digiacomo, Ledesma, & González-Rosa, 2008). Developmental studies of orienting attention using Posner's cueing paradigm have found that both 6–13 years old children and adults show higher P1 amplitude on validly cued trials, whereas latencies of P3 appeared delayed for children with respect to adults under invalid conditions (Flores, Gómez, & Meneres, 2010; Perchet & García-Larrea, 2000).

Finally, several electrophysiological indexes have been associated with executive control processes. Congruency of distracting stimuli in a flanker task modulates the N2, a negative fronto-parietal component that peaks approximately 200–400 ms post-target. This effect has been related to control processes arising in the anterior cingulate cortex (van Veen & Carter, 2002). N2 amplitude increases in incongruent trials relative to congruent trials, signaling greater effort to suppress irrelevant information in the incongruent condition. In fact, smaller N2 effect has been associated with greater efficiency of executive control over and above the effect of age (Lamm, Zelazo, & Lewis, 2006; Stieben et al., 2007). Several developmental studies carried out with children as young as 4 years of age have observed conflict-related amplitude modulation of ERP components. Before age 6 years, children show very weak conflict-related modulation in the latency of the N2 (Ladouceur, Dahl, & Carter, 2007; Rueda, Posner et al., 2004). However, young children show larger conflict-related amplitude effects compared to adults in later latencies, from about 600 to 800 ms post-target in anterior mid-frontal leads (Rueda, Posner et al., 2004). From about 6 to 8 years of age, the conflict-related amplitude effects are observed in more adult-like latencies, and the size of the effect appears to decrease with age (Jonkman, 2006; Lewis & Todd, 2007).

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